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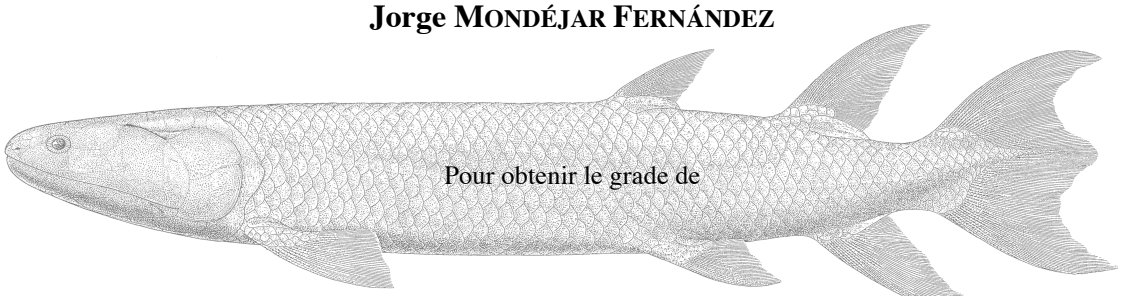
# STRUCTURE AND DEVELOPMENT OF THE SCALES AND FIN RAYS IN VERTEBRATES AND THEIR EVOLUTION IN SARCOPTERYGIANS DURING THE 'FISH-TETRAPOD TRANSITION'

par

**Jorge MONDÉJAR FERNÁNDEZ**



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# Structure and development of the scales and fin rays in vertebrates and their evolution in sarcopterygians during the 'fish-tetrapod transition'

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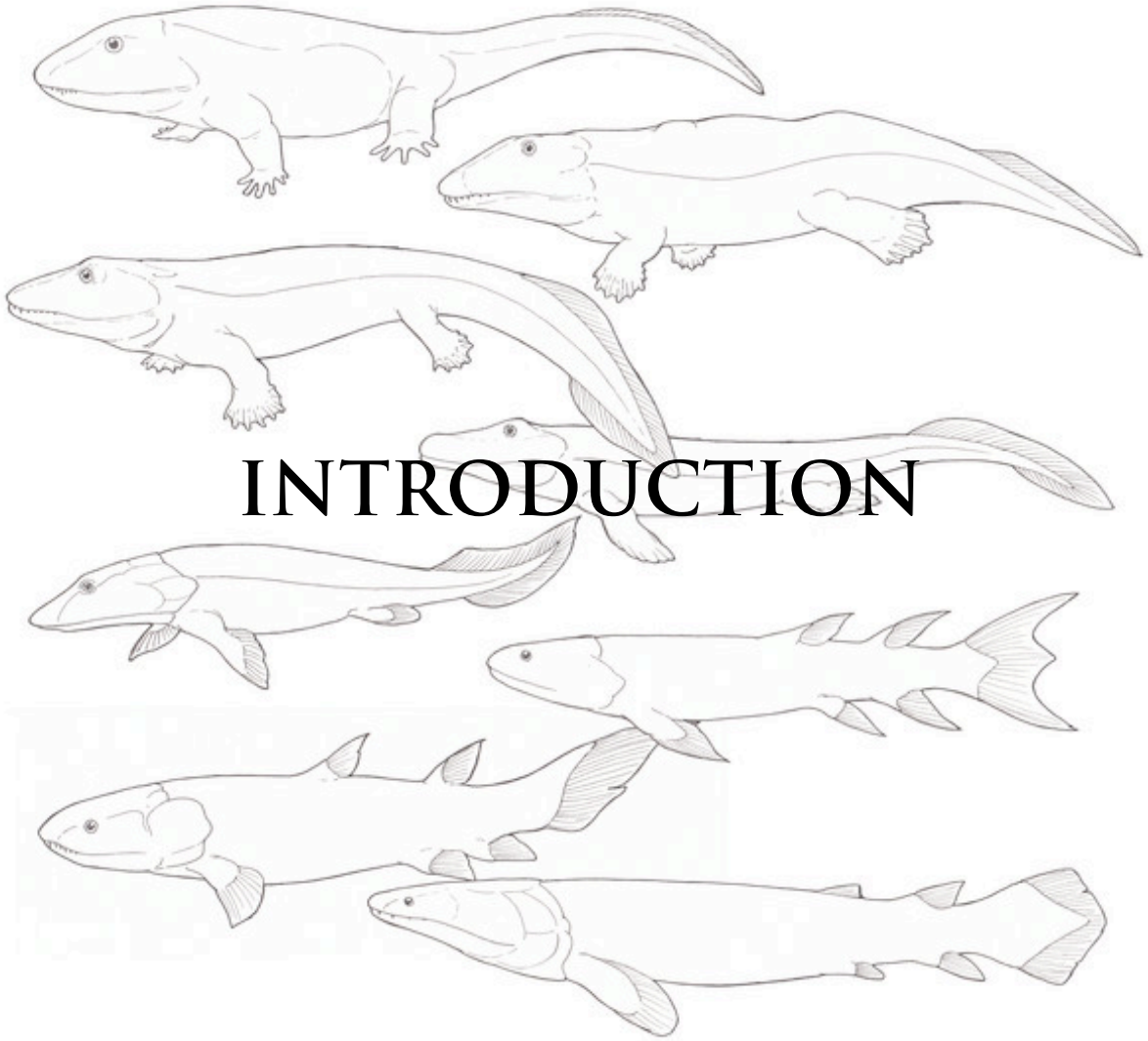
*If there is one thing history of evolution has taught us,*
*is that life will not be contained.*
*Life breaks free.*
*It expands to new territories*
*and crashes through barriers painfully*
*may be even… dangerously but and…*
*well there it is.*

Ian Malcolm



# INTRODUCTION

# I. GENERAL INTRODUCTION

The origin of tetrapods in the Devonian period is one of the most fundamental episodes in the evolutionary history of vertebrates. The implications of the 'fish-tetrapod transition' are tremendous, as tremendous are all the morphological, physiological, and behavioural differences between fishes* and land vertebrates. In this thesis I have narrowed the scope of studying the different aspects of this transition to tackle the precise question of the evolution of two components of the dermal skeleton of vertebrates: the scales and the fin rays.

The evolution of the scales and fin rays in Devonian tetrapods is still a rather unexplored aspect of the 'fish-tetrapod transition'; and yet the structural and developmental significances of the changes that took place during the transition from sarcopterygian fishes to tetrapods marked the evolution of limbed vertebrates during the Carboniferous and, somehow, enabled their definitive transition to land. Indeed, the skin and the associated dermal ossifications were key structures involved in fundamental aspects of the metabolism, way of life, and locomotion of sarcopterygian fishes and early tetrapods. Their study can thus be considered as highly informative in order to better understand all the major aspects of the 'fish-tetrapod transition'.

This thesis will be divided into several chapters. In the introduction (Chapter I) I will set the scene of the 'fish-tetrapod transition' and present the time and ecological frame of this study, the definition of taxonomical groups and the anatomical and histological terms used in throughout this thesis. The studied, handled, sectioned and/or

* For general convinience, in this study I will consider as "fishes" the paraphyletic assemblage of all non tetrapod aquatic vertebrates.

figured material and the different methodologies and techniques of study will then be described (Chapter II). The results will be presented as a series of Papers divided into the scales (Chapter III) and the fin rays (Chapter IV). The discussion (Chapter V) will try to synthesize the scientific contribution of this thesis to the field of vertebrate palaeontology and evolutionary biology and will be followed by the conclusion and perspectives (Chapter VI). Finally, the Bibliography will include all the references cited in the main text. The Appendices will include a series of articles that were written during the course of this thesis but that are not part of the present dissertation, among other complementary information.

In the following, and rather extensive, sections I will introduce all the basic and essential information to follow the present dissertation, and I apologize in advance for the length of certain parts, which I, nevertheless, consider necessary to the understanding of this work. First, I shall 'set the scene' of the thesis and establish the chronological, paleogeographic, and ecological framework of the early evolution of sarcopterygians and the 'fish-tetrapod transition'. Then I will detail the systematics of the Sarcopterygii and describe the main morphological features of the sarcopterygian anatomy discussed throughout this thesis. Next, I will focus on the 'fish-tetrapod transition' proper and present the main aspects of study of this crucial evolutionary episode, both under the point of view of palaeontology and developmental biology. Finally, I shall review the most important evolutionary aspects of the dermoskeleton and furnish the definition of the main terms used in the Papers and in the main text dealing with scale and fin ray function, development, structural diversity, and evolution.

## II. THE DEVONIAN

The Devonian period has been traditionally referred to as the 'Age of Fishes'. This appellation is appropriate given the dramatic evolutionary changes occurred in all of the main fish lineages during this period (e.g., "agnathans", "placoderms", chondrichthyans, "acanthodians", and osteichthyans) that experienced rapid diversification peaks throughout the Devonian, despite an earlier appearance in the fossil record (e.g., Cambrian and Ordovician for the majority of "agnathans" and Silurian for the gnathostomes). The Devonian is not only a crucial stage in the evolution of vertebrates, but was also an inflexion point for the ensemble of life on Earth; accordingly, the Devonian period is better defined as the 'Age of Changes'.

Plants played a major role in this Devonian transformation of ecosystems through the emergence and diversification of vascular plants. Their evolution and continental expansion throughout the Devonian not only durably transformed the landscape but also modified the relationships between bio- and geosphere by transforming the terrestrial environment and linking it more closely with the aquatic realm (ALGEO *et al.*, 1998). The first forests appeared in the Devonian and created a totally new biome (STEIN *et al.*, 2012). Soil formation was accelerated by the intense development of roots and terrestrial habitats became more diverse and stable (SHEAR, 1991) at the same time as freshwater and estuarine environments diversified and became more productive (CRESSLER *et al.*, 2010). The effects of plant evolution and establishment on land had a considerable effect in global carbon cycling and the Devonian extinction crisis (STREEL *et al.*, 2000). Ultimately, these changes also set the stage for the evolution of tetrapods and their colonization of land (CLACK, 2007).

## II.1. STRATIGRAPHY

The Devonian is a geological period of the Primary era (or Palaeozoic) generally dated between 420 and 360 million years (419.2 to 358.9 million years according to the INTERNATIONAL COMMISSION ON STRATIGRAPHY, ICS, 2012). It is preceded by the Silurian and followed by the Carboniferous. The Devonian period is divided into three epochs, in turn divided into several stages: Early Devonian (Lochkovian, Pragian, and Emsian), Middle Devonian (Eifelian and Givetian), and Late Devonian (Frasnian and Famennian) (Fig. II.1.1).

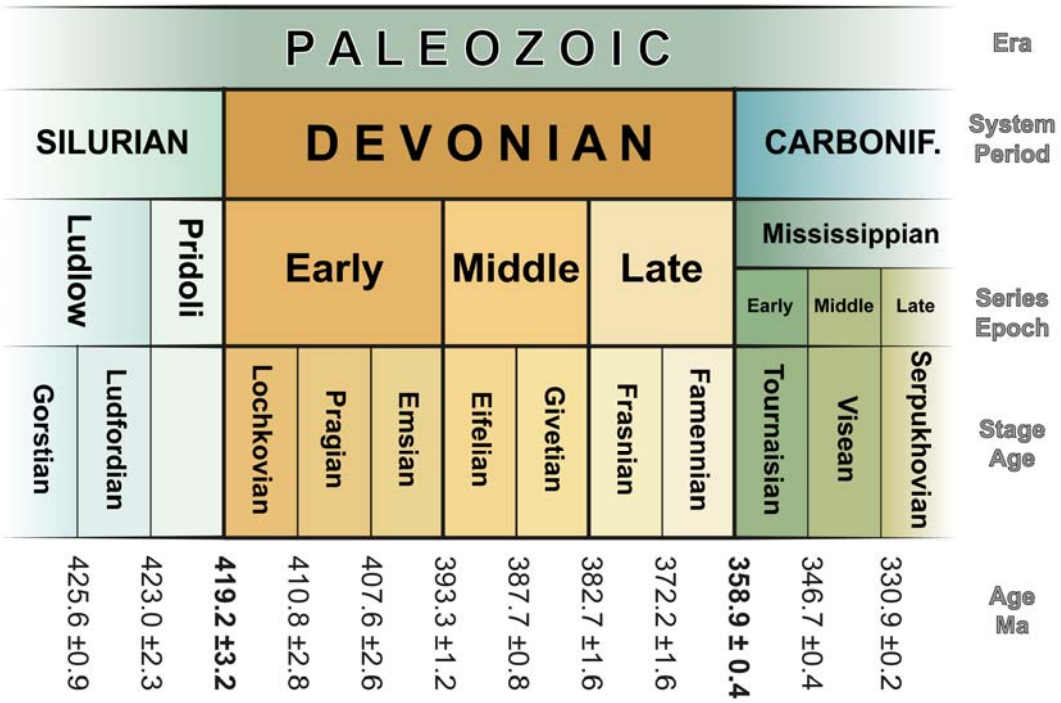



**FIGURE II.1.1. Devonian chronostratigraphy**. After the INTERNATIONAL STRATIGRAPHIC CHART, August 2012).

Its name comes from the region of Devonshire (England) where numerous rock outcrops dating from this period have been found and studied since the nineteenth

century (e.g., MILLER, 1841). Devonian sediments are also found worldwide (e.g., Europe, United States, Greenland, South America, Middle East, China, Australia, etc.). The vertebrate-bearing sediments correspond to a large diversity of facies, from marine to terrigenous sedimentary depositions (sand, silt, etc.) produced by shallow marine, large deltas, and lacustrine environments (e.g., CRESSLER *et al.*, 2010).

## II.2. PALEOGEOGRAPHY

Significant changes in the world's paleogeography took place during the Devonian. At that time, the arrangement of continents was very different from today. The masses resulting from the break-up of Cambrian Pangea were re-associating and began to build the future Permo-Triassic Pangea.

During the Early Devonian, two major landmasses were arranged to form two supercontinents: Euramerica (in the North) and Gondwana (in the South). Other small blocs were more or less associated either with Euramerica (e.g., Siberia and Kazakhstan) or with Gondwana (e.g., Northern and Southern China, Eastern Asia). A vast ocean, the Panthalassa, covered the rest of the globe surface (Fig. II.2.1).

The northern hemisphere was occupied by the super continent Euramerica (or Laurussia) formed by the provinces of Baltica (currently comprising Scandinavia, European Russia, and the British Isles) in the east, and Laurentia (North America, Greenland, and the Svalbard archipelago) in the west. Both blocks collided during the Silurian resulting in the closure of the Iapetus Ocean and originating the Caledonian Orogeny that formed the mountain ranges of the actual Scandinavia, Northern England and the Appalachians in the eastern United States. The rapid erosion of these mountains, at this time located at the equator, resulted in the deposition of the red sediments

known as the "old red sandstone", which are characteristic of the Devonian outcrops in Europe and North America.

In the southern hemisphere, the super continent Gondwana, comprising South America, Africa, Australia, India and Antarctica, occupied a vast area. This large block pivoted and moved northwards throughout the Devonian and finally contacted Euramerica in the latest Famennian, closing the western branch of the Rheic Ocean and forming the first stages of Pangea. At the same time, the Paleothetys Sea was beginning to take shape as a result of the northward drift of eastern Gondwana blocks (i.e., China and Middle East blocks).

Nevertheless, Devonian paleogeographic representations are far from consensual. The reconstructions are mainly based on paleomagnetic data and geographic distribution of biological populations. The current absence of seafloor dating from before the formation of the Triassic Pangea complicates paleomagnetic reconstructions, which are only informative on the latitude. Longitude can be inferred from paleobiogeographical data, however, interpretations of biogeographic distributions are often in conflict with geological patterns (e.g., DUPRET *et al.*, 2011).

A great number of paleogeographical studies show an important variability concerning the arrangement of landmasses, particularly in relation to the paleoequator. The paleomagnetic interpretations (Fig. II.2.1, BLAKEY, 2011; GOLONKA, 2000) reconstruct Euramerica as an overall vertically elongate landmass, with its main surface (Baltica and Laurentia) located in both sides of the equator, while palynological studies place Euramerica completely under the equator, closely contacting Gondwana (e.g., STREEL *et al.* 2000). On the other hand, Gondwana is usually reconstructed as a broad supercontinent horizontally spreading across the southern Hemisphere.

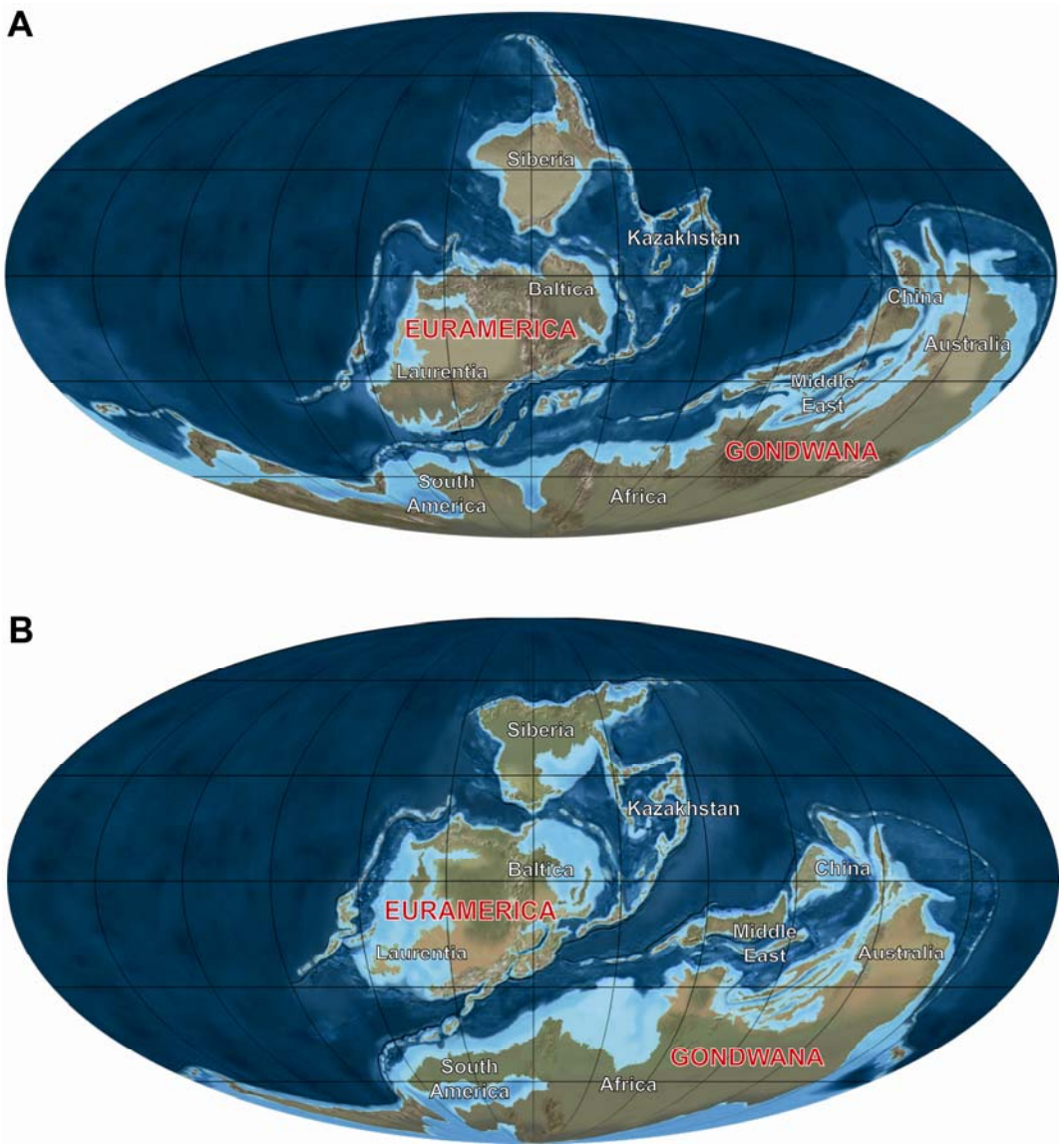



**FIGURE II.2.1. Devonian paleogeographic maps. A**. Early Devonian (Emsian, around 400 million years); **B**. Late Devonian (Famennian, around 370 million years). Modified after BLACKEY, 2011.

Despite this lack of consensus, the organization of the Devonian world in two super continents is maintained in the vast majority of studies, along with the relative distribution of rather large landmasses (Gondwana and Southern part of Euramerica) in the Southern Hemisphere and along the equator.

### II.3. CLIMATE AND SEA LEVEL

The Devonian was formerly considered as a warm and dry period, with a rather uniform deviation of temperatures. However, since the 1990's new studies have shown that there were variations of the global climate throughout the period (ALGEO *et al.*, 1998; STREEL *et al.*, 2000) (Fig. II.3.1).

Paleoclimatic data, fossil distribution, and paleobiogeographic trends show that each of the stages of the Devonian had different and specific climatic conditions (after MCGHEE, 1996):

- **Early Devonian**: the climate was globally hot and dry. Temperate oceans with a low latitudinal gradient of temperatures could have allowed the migration of marine fish faunas between Gondwana and Euramerica. Numerous marine transgressions formed shallow shelf seas in both hemispheres.
- **Middle Devonian**: the climate was warm and becoming wetter. The first accumulations of coal at the equator date from this time and are associated with the progressive dispersal and colonization of tropical environments by land plants. The relative paleoposition of Gondwana and Euramerica would have produced a particular atmospheric and oceanic circulation producing monsoons and creating a savanna-like region with a strong seasonality along the tropics.
- **Late Devonian**: the climate was becoming cooler and wetter. Mountain glaciers, and probably also shield glaciers, developed in the southern hemisphere and suggest a major latitudinal temperature gradient during that time. Forest formations were increasing in the tropical region as evidenced by large deposits of coal at the equator. The marine environment suffered a series of successive biological crises associated with marine regressions and water anoxia during the Famennian.

It is also known that concentrations of atmospheric gases ($CO_2$ and $O_2$) fluctuated dramatically during the Devonian (DAHL *et al.*, 2010) (Fig. II.3.1). Carbon dioxide ($CO_2$) is a greenhouse gas that plays a key role in the variations of global temperature; variation in atmospheric $CO_2$ levels have dramatic consequences in global warming and cooling of the Earth's surface. It is logical to suppose that the Devonian period passed from being warm to a cool and temperate as a result of a prolonged decrease in atmospheric $CO_2$.

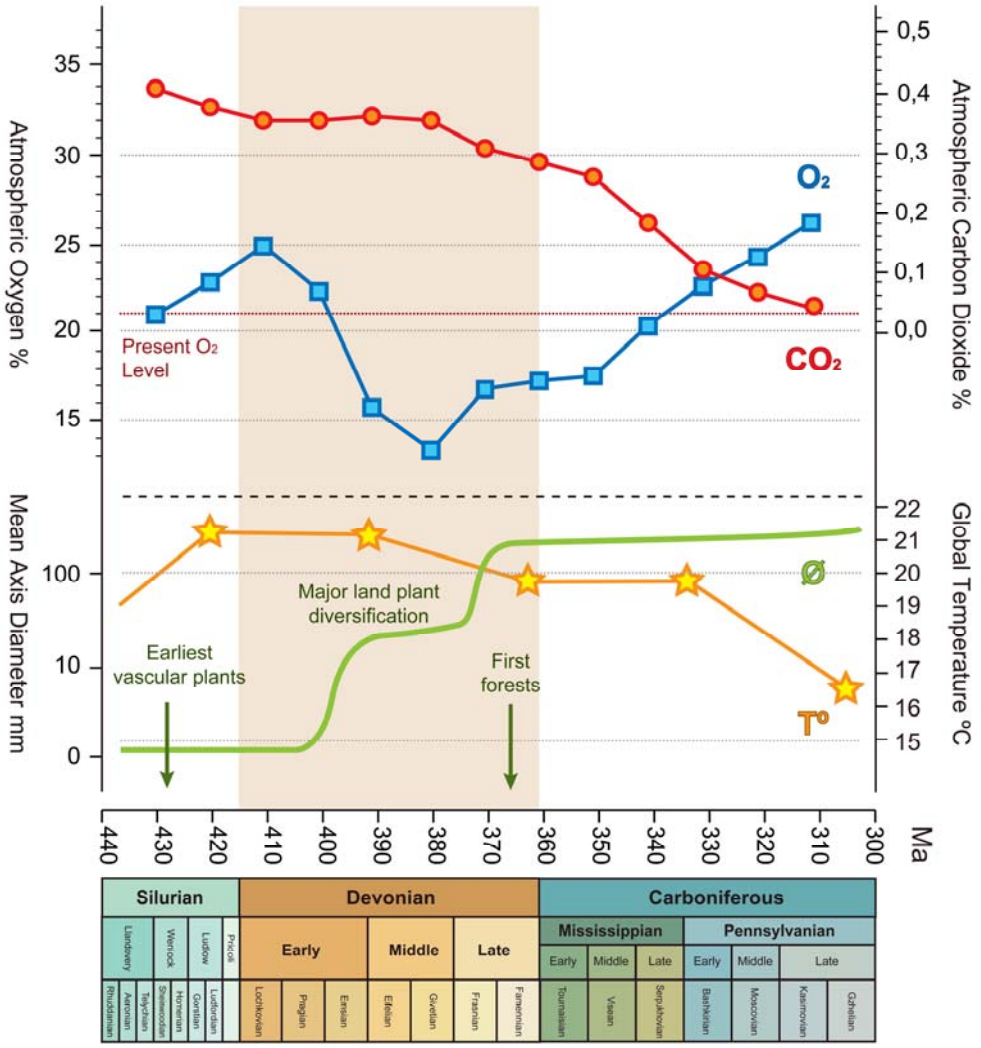



**FIGURE II.3.1. Graphs of atmospheric levels of oxygen ($O_2$) and carbon dioxide ($CO_2$), plant stem diameters (Ø), and average global temperatures ($T^o$)** placed on the same time scale of the Middle Palaeozoic. Brown-shaded rectangle shows the time extension of the Devonian Period. Modified after CLACK, 2007; WARD *et al.*, 2006.

The Devonian was subject to intense sea level changes that produced many sedimentary basins as shallow shelf seas spread over the continental margins during marine transgressions. The extreme sea level fluctuations of the Devonian must have profoundly influenced faunal and floral distributions, isolating land areas during transgressions and inhibiting the dispersal of continental biota, and eliminating shallow marine shelf environments during regressions (YOUNG, 2003). COPPER (1986) noted the much higher sea levels of the late Frasnian compared to today (60-100 m higher), which resulted in extensive flooding of the paleocontinents by shallow seas. He also suggested the closure of the ocean between Gondwana and Euramerica as a mechanism for interrupting circumequatorial warm water currents during the Frasnian, leading to global cooling in the Famennian (COPPER, 1986). The sea-level maximum in the latest Frasnian, and the major regressions of the early Famennian, which are related to the Late Devonian glaciations are considered to be associated with the faunal extinctions at the Frasnian-Famennian boundary.

## II.4. FAUNAL IMPLICATIONS

### II.4.1. THE 'GREAT DEVONIAN INTERCHANGE'

A significant faunal exchange between Euramerica and Gondwana during the Middle–Upper Devonian is now widely accepted by many researchers, but the details depend on better documentation of Gondwanan taxa (YOUNG, 2008). Current knowledge on vertebrate biogeographic relationships between Euramerica and Gondwana states that the 'Great Devonian Interchange' (MCGHEE, 1997; YOUNG, 2006) at the Frasnian-Famennian boundary involved three major vertebrate groups expanding from Euramerica to Gondwana (tristichopterids, holoptychiids, and tetrapods), and five

groups of Gondwanan origin extending their range into Euramerica (phyllolepid and groenlandaspid placoderms, gyracanthid acanthodians, and rhizodontid and megalichthyid sarcopterygians) (e.g., JOHANSON & AHLBERG, 1998; CLÉMENT *et al.*, 2004, JANVIER & CLÉMENT, 2005); however, the precise location of the contact between Euramerican and Gondwanan landmasses is still uncertain (JANVIER *et al.*, 2007).

YOUNG (e.g., 1993, 2003) identified a worldwide biogeographic trend for the vertebrate faunas during the Devonian, with an Early Devonian endemism breaking down into a Late Devonian cosmopolitanism. Examples of tetrapodomorphs (e.g., rhizodontids and ‘‘osteolepiforms’’, among others) are consistent with this general pattern (JOHANSON, 2004) and have even stretched the switch from endemism to cosmopolitanism to the Middle Devonian. Indeed, evidence of sarcopterygian dispersal during the Middle–Upper Devonian is complemented by similar placoderm distribution patterns in space and time (YOUNG, 2008; YOUNG *et al.*, 2010).

This faunal spread between landmasses could have been favoured by the sea-level maximal in the late Frasnian before the great early Famennian regression (YOUNG, 2003). Indeed, as Pangea formed, the supercontinents of Euramerica and Gondwana were brought together around the Southern tropics, destroying the near-shore and marine habitat and facilitating migration between once isolated faunas (COPPER, 1986). Euramerican regional biota could have been swept away by southern migrations during the faunal interchange with Gondwana (CLÉMENT *et al.*, 2004; JANVIER & CLÉMENT, 2005; CLACK, 2006). Gyracanthid acanthodians and rhizodontid and megalichthyid sarcopterygians might have caused turnover in previously isolated ecosystems by outcompeting or preying upon placoderms, porolepiforms, and early tetrapods (CLÉMENT *et al.*, 2004; CLACK, 2006). Soon after the Devonian, marine durophagous “placoderms” and sarcopterygians were replaced by holocephalans and actinopterygians, respectively

(BLIECK, 2011). However, even considering the possibility of global turnover, change was usually assumed to be gradual and limited to the marine realm. Freshwater environments, by contrast, might have act as a refugium for large fish faunas (FRIEDMAN & SALLAN, 2012).

### II.4.2. THE LATE DEVONIAN BIODIVERSITY CRISIS

It has long been apparent that the vertebrate fauna changed over the latest Devonian into the Carboniferous, setting the transition from the so-called 'Age of Fishes' to the 'Age of Amphibians'. It is now known that a series of marine mass extinctions occurred at the end of the Devonian; however their timing and duration are still subject to considerable debate and a variety of interpretations. These extinctions encompass a time span of 25 million years and are known as the 'Late Devonian Biodiversity Crisis' (STIGALL, 2010).

The most heavily investigated of these successive extinction episodes is the Kellwasser event, dated around the Frasnian–Famennian boundary (374.5 Ma), that was linked to the supposed loss of 60 per cent of genera and up to 82 per cent of species (MCGHEE, 1996), and accordingly has been placed among the Big Five mass extinction events (RAUP & SEPKOSKI, 1982). However, large events have also been identified at the end-Givetian (the Taghanic event, 385 Ma) and at the latest-Famennian (the Hangenberg event, 359 Ma, now designated as the Devonian-Carboniferous boundary) (FRIEDMAN & SALLAN, 2012). Although less brutal than the Kellwasser event, the Hangenberg is of particular interest for marine fishes since it was responsible of the loss of around 44 per cent of major gnathostome clades (MCGHEE, 1996; SALLAN & COATES, 2010) and seriously affected the sarcopterygians.

Conodonts, armoured agnathans (e.g., heterostracans, osteostracans, galeaspids, and thelodonts) and various groups of gnathostomes (e.g., numerous placoderm and acanthodian, actinistian, and actinopterygian families) are counted among the victims of the Kellwasser extinctions (374.5 Ma). However, there does not seem to be evidence indicating a single, sudden vertebrate extinction event at the Frasnian–Famennian boundary. Instead, differences between Frasnian and Famennian faunas were the culmination of millions of years of gradual environmental and faunal change leading to low taxonomic diversity and subsequent decline (FRIEDMAN & SALLAN, 2012).

The Hangenberg event (359 Ma), however, appears to represent a real, abiotically driven mass extinction (FRIEDMAN & SALLAN, 2012). Formation of glaciers, probably at sea level at both the poles and near the tropics, might have been related with a drop in atmospheric $CO_2$ values (Fig. II.3.1), which resulted in an important worldwide marine regression. The Hangenberg extinctions at the Devonian-Carboniferous boundary whipped out the remaining groups of "placoderms" and ischnacanthid acanthodians, and deadly hit the sarcopterygians with the extinction of porolepiforms, onychodontids, "elpistostegalians", a few "osteolepidids" families, and marine lungfishes. The Hangenberg event seriously affected and modified the habitat ranges and environmental associations of gyracanthids, elasmobranchs, rhizodontids, and tetrapods that might have to find refuge in new fresh-water environments (FRIEDMAN & SALLAN, 2012).

After the Devonian, the Early Carboniferous (Tournaisian) faunas are characterized by a highly homogeneous assemblages dominated by actinopterygians and chondrichthyans, with fewer lungfishes, rhizodontids, megalichthyids, actinistians, "acanthodians", and scant tetrapod material (COATES & CLACK, 1995; COATES *et al.*, 2008; SALLAN & COATES, 2010). The Romer's Gap is interpreted as the post-Hangenberg

recovery interval and is considered a bottleneck in tetrapod phylogeny (RUTA *et al.*, 2003; COATES *et al.*, 2008). The Tournaisian marks the beginning of a major round of diversification for the main surviving clades, i.e., actinopterygians, chondrichthyans, and tetrapods, that knocked the new ecological opportunities facilitated by the faunal vacuum at all ecological levels. It is not clear why other survivors, like "acanthodians" and large tetrapodomorph fishes (e.g., rhizodontids and megalichthyids), did not diversify into new ecospaces during and after the Carboniferous (JANVIER, 1996; SALLAN & COATES, 2010) but rather persisted for several million years before disappearing.

In summary the Late Devonian extinctions, and more particularly the Hangenberg event, seem to have restructured vertebrate ecosystems worldwide and marked a bottleneck in the evolution of modern clades such as tetrapods. The environmental changes certainly drove the evolution of features involved in the physiology and locomotion of sarcopterygians (GRAHAM *et al.*, 1995, 1997); the dermal scales and fin rays are thus a suitable mean to understand the extend of the relationship between morphological and environmental changes.

# III. THE SARCOPTERYGIANS

Sarcopterygii (from the Greek “sarx”=flesh and “pteryx”=fin or wing) comprise the so-called lobe-finned fishes and the tetrapods. Sarcopterygian fishes are chiefly characterized by the monobasal articulation of their paired fins formed by a single articulated element (the humerus for the pectoral fin and the femur for the pelvic fin), among other cranial and histological features. An important set of muscles is well developed at the base of both paired and median fins; hence sarcopterygians owe their name to their fleshy fins.

## III.1. SARCOPTERYGIANS GENERALITIES

Sarcopterygians were highly diversified during the Devonian, but today only three groups survive: the actinistians or coelacanths (one genus, *Latimeria*, with two species), the dipnoans or lungfishes (three genera, *Neoceratodus*, *Lepidosiren* and *Protopterus*, with six species), and the tetrapods (approximately 30.000 species) (LECOINTRE & LE GUYADER, 2001).

Classically it is considered that the Sarcopterygii comprise seven orders, most of them of doubtful monophyly, which are as follows: Onychodontida, Actinistia, Porolepiformes, Dipnoi, Rhizodontida, Osteolepiformes, Elpistostegalia and Tetrapoda (Fig. III.1.1) (JANVIER, 1996) (considerations on the monophyly of these groups will be presented later). The interrelationships of sarcopterygians are still much debated (e.g., CLOUTIER & AHLBERG, 1996; ZHU & SCHULTZE, 1997; FRIEDMAN, 2007a; ZHU *et al.*, 2009), specially the basal part of the tree and the position of the onychondontids relative to actinistians.

However, the upper part of the tree is normally well defined in the vast majority of phylogenetic analyses. The broad phylogenetic framework of the Sarcopterygii comprises two large monophyletic groups: the Dipnomorpha (including the dipnoans and their closest relatives, the porolepiforms), and the Tetrapodomorpha (comprising all sarcopterygians more related to tetrapods than to dipnoans) (AHLBERG, 1991) (Fig. III.1.1).

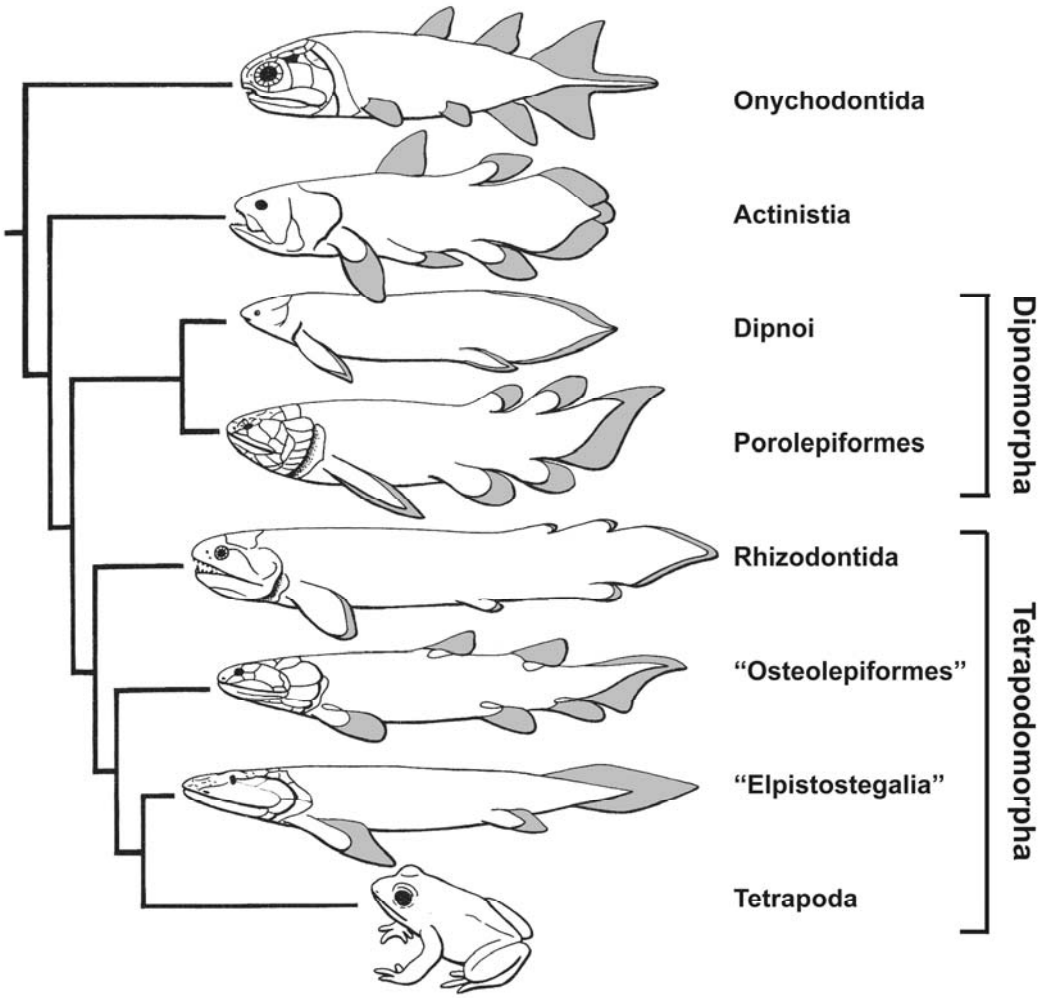



**FIGURE III.1.1. Interrelationships of the Sarcopterygii**, illustrating the main phylogenetic framework followed in this thesis. Stem sarcopterygians not shown. Modified after JANVIER, 1996.

A sarcopterygian fish can be easily recognized amongst fossil and extant faunas based on a proper knowledge of its general anatomy. Sarcopterygians are characterized by being relatively long-bodied animals with a skull with a hinged braincase that is divided into a front section (ethmosphenoid region) and a rear section (otoccipital region). This flexure within the braincase is reflected in the skull roof bones of each clade showing a parietal and a post-parietal shield separated by the intracranial joint. Some derived members have the intracranial joint immobilized by a fusion of bones between the parietal and the post-parietal shields (e.g., dipnoans, "elpistostegalians" and early tetrapods). The extant coelacanth *Latimeria* is the only living vertebrate to posses a hinged braincase with an intracranial joint.

Concerning their postcranial anatomy, all groups of sarcopterygian fishes show a rather stable fin pattern. The paired fins (pectoral and pelvic) show the characteristic monobasal articulation as previously described. The median fin pattern comprises generally two dorsal fins, an anal fin, and a caudal fin (or tail). Dorsal and anal fins can be lost or modified in certain lineages (e.g., dipnoans, "elpistostegalians", and tetrapods). The caudal fin is supposed to be primitively heterocercal but tends to become diphycercal in almost all groups (e.g., onychodontids, actinistians, dipnoans, rhizodontids, "osteolepiformes", "elpistostegalians", and tetrapods). Each fin is composed of a basal endoskeleton and a distal dermoskeleton. The osseous dermal skeleton is composed of osseous fin rays (lepidotrichia) that are generally jointed and branched and articulate with the endoskeleton (see Paper IV for further details).

Perhaps owing to their significance in understanding the origin of tetrapods, Palaeozoic sarcopterygians seem to have been more thoroughly investigated than actinopterygians. However, sarcopterygians display a wider range of morphological diversity than actinopterygians, even at the level of their internal anatomy (JANVIER,

1996). The anatomically best-known Devonian sarcopterygians were for long the "osteolepiform" *Eusthenopteron* (e.g., JARVIK, 1944a,b, 1957, 1980; ANDREWS & WESTOLL, 1970a), the porolepiform *Glyptolepis* (ANDREWS & WESTOLL, 1970b; AHLBERG, 1989), and the actinistian *Diplocercides* (STENSIÖ, 1937; JESSEN, 1973), which had been investigated by the grinding section method, as well as, to some extent, the tetrapod *Ichthyostega* (JARVIK, 1952, 1996). Since the late 90's our knowledge on the anatomy of other Devonian sarcopterygian taxa has been greatly extended with the descriptions of the onychodontid *Onychodus* (ANDREWS *et al.*, 2006), the "osteolepiforms" *Cladarosymblema* (FOX *et al.*, 1995), *Medoevia* (LEBEDEV, 1995), *Gogonasus* (LONG *et al.*, 1997, 2006), the "elpistostegalian" *Tiktaalik* (DAESCHLER *et al.*, 2006; SHUBIN *et al.*, 2006; DOWNS *et al.*, 2008), and the tetrapod *Acanthostega* (COATES, 1996; CLACK, 2002a,b, 2003).

The earliest known sarcopterygians date from the Siluro-Devonian boundary and are represented by the enigmatic Chinese taxa *Guiyu* (Ludlow, Late Silurian) (ZHU *et al.*, 2009), *Psarolepis* and *Youngolepis* (Lockhovian, Early Devonian) (CHANG, 1982; YU, 1998; ZHU & SCHULTZE, 1997). Aside from stem sarcopterygians (Fig. III.1.1, 2), the supposedly more primitive taxa, such as onychodontids and actinistians, strangely appear somewhat later, in the late Early Devonian. The recent discoveries of the onychodontid *Qingmenodus* from Pragian of China (LU & ZHU, 2010) and the actinistian *Eoactinistia* from the Pragian of Australia (JOHANSON *et al.*, 2006) has pushed back the earliest record of both groups.

Dipnomorphs are known since the Early Devonian, represented by the stem dipnomorph *Youngolepis* from the Lockhovian and Pragian of China (CHANG & YU, 1981; ZHU & FAN, 1995). Tetrapodomorphs are represented since the end of the Early Devonian by *Kenichthys* from the Emsian of China (CHANG & ZHU, 1993). "Osteolepiforms" first appear at the beginning of Middle Devonian times, represented by

taxa such as *Osteolepis* from Scotland (JARVIK, 1948), whereas rhizodontids, "elpistostegalians", and tetrapod remains are not known before the Frasnian.

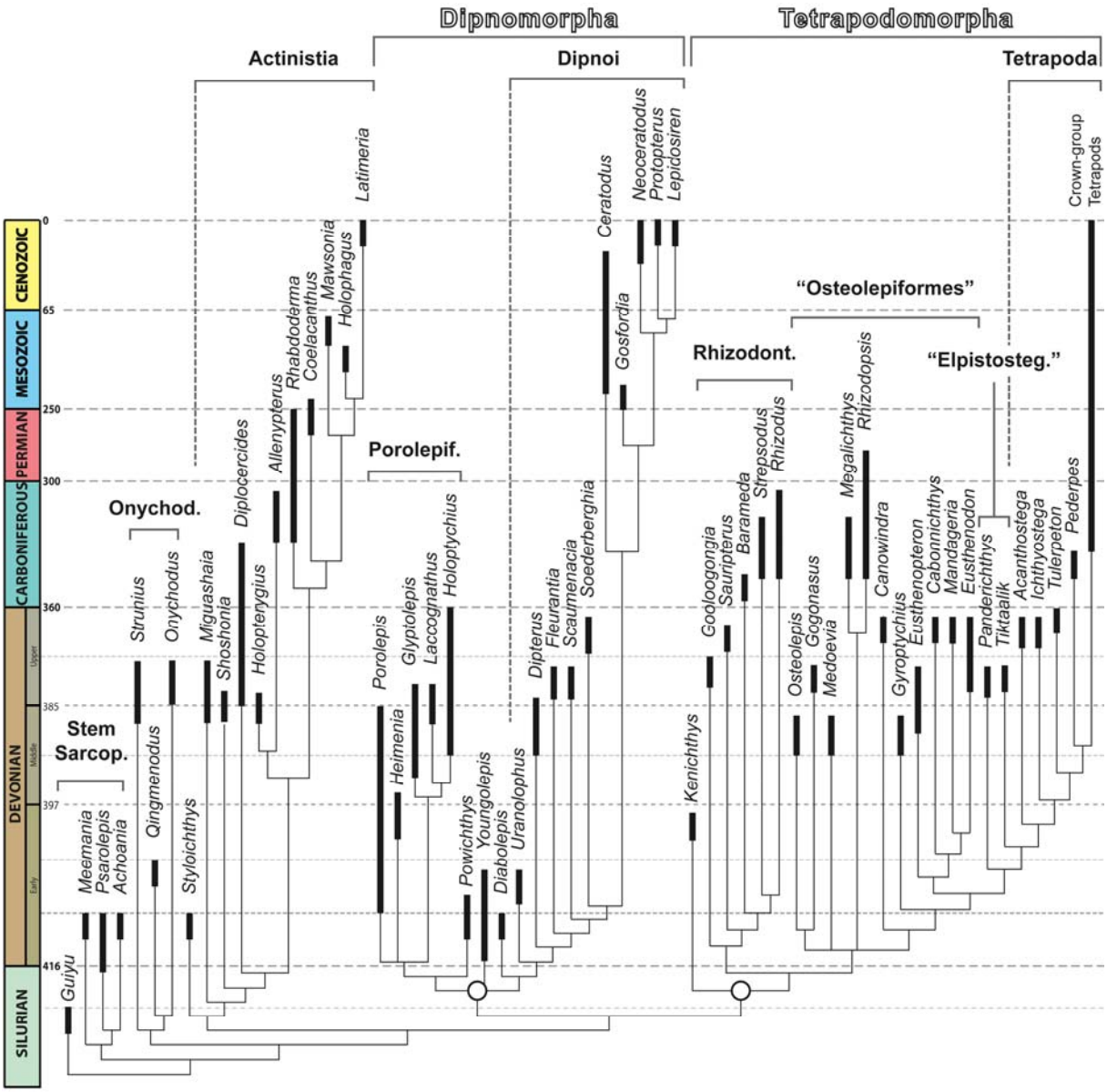



**FIGURE III.1.2. Consensual cladogram of sarcopterygian interrelationships** illustrating the main taxa discussed in this thesis. The dates of origin of clades are hypothetical. Phylogenetic hypothesis after JANVIER, 1996; AHLBERG & JOHANSON, 1998; JOHANSON & AHLBERG, 2001; CLÉMENT, 2001b; ZHU *et al.,* 2001, 2006, 2009; SCHULTZE, 2004; FRIEDMAN, 2007a; FRIEDMAN *et al.*, 2007; SNITTING, 2008a,b; COATES *et al.*, 2008; LU & ZHU, 2010, among others.

It is thus clear that the stratigraphical distribution of sarcopterygians does not match closely the currently accepted pattern of their interrelationships (Fig. III.1.2) and that the occurrence of ghost lineages in sarcopterygian phylogeny is becoming more and more common with every new discovery. One example of this is the recent finding of the 'Early-Middle Devonian tetrapod Poland tracks' (NIEDZWIEDZKI *et al.*, 2010) that has significantly changed our ideas on the timing of tetrapodomorph and early tetrapod evolution since these tracks predate the oldest tetrapod skeletal remains (e.g., *Elginerpeton*) by 18 millions years and, more surprisingly, the earliest "elpistostegalians" (e.g., *Panderichthys*) by about 10 million years (JANVIER & CLÉMENT, 2010). This indicates that most of the early history of each sarcopterygian group occurred much earlier than their earliest fossil record, e.g., during the Silurian for the basal most sarcopterygians and in the Middle or even Early Devonian for tetrapods and their immediate ancestors, which offers new and exiting possibilities of fossil site survey.

## III.2. SARCOPTERYGIANS AS OSTEICHTHYANS

The Osteichthyes (from the Greek "osteon"=bone and "icthyo"=fish, thus 'bony fishes') form the largest and most diverse group of extant vertebrates. Osteichthyans are divided in two major clades: the Actinopterygii ('ray-finned fishes') and the Sarcopterygii ('lobe-finned fishes'), thus including the tetrapods. If we are to study the origins of sarcopterygian morphology, and therefore the deep origin of the tetrapod anatomy, we first need to identify the characters uniting lobe-finned with ray-finned fishes.

Osteichthyans appeared probably during the Silurian and were then a reduced component of the fish faunas mainly dominated by “agnathans” and “placoderms”. By the start of the Devonian, the group had already split into the two well-defined clades of actinopterygians and sarcopterygians; from this point on both lineages will follow very different evolutionary paths. During the Devonian osteichthyans reached high diversity peaks and before the end of the Devonian they had replaced the “placoderms” as the dominant predatory gnathostome component of fish faunas. Among these extraordinary Devonian adaptive peaks of diversity, tetrapods evolved from aquatic sarcopterygians, less than 150 million years after the origin of osteichthyan fishes. However, despite a well-represented Devonian fossil record, the importance of sarcopterygians diminished after the Devonian at the same time as actinopterygians initiated their own diversification (LONG, 2011).

The key-defining feature of osteichthyans is the endochondral bone formed around a cartilage precursor that builds their solid internal skeleton. There a many other features unique to osteichthyans but they will not be detailed here (see FRIEDMAN & BRAZEAU, 2010). However the question of the degree of generality of endochondral bone is still debated (JANVIER, 1996) and fossil evidence attest that the earliest representatives still show a dominant exoskeleton against the endoskeleton along with a lesser degree of ossification. Therefore, the dermal skeleton, and notably the squamation have proven to be of capital importance in the systematic studies of early osteichthyans (BOTELLA *et al.*, 2007; CUNNINGHAM *et al.*, 2012). Different scale-related features have been considered characteristic either to sarcopterygians (cosmine) or actinopterygians (ganoine, anterodorsal process and slender peg-and-socket articulation). However, the demarcation between actinopterygians and sarcopterygians becomes obscure, when we consider basal osteichthyans (CHEN *et al.*, 2012).

Gnathostomes primitively have dermal and endoskeletal elements in both pectoral and pelvic girdles and it was assumed that the dermal pelvic elements were secondarily lost in osteichthyans. The new discoveries of dermal elements (fin spines) in the pectoral and pelvic fins of stem sarcopterygians (e.g., *Guiyu* and *Psarolepis*) (ZHU *et al.*, 2009, 2012a) suggest that in sarcopterygians, the loss of dermal pelvic girdles occurred at the internode between stem sarcopterygians and sarcopterygians crownward to onychodontids and actinistians, and thus must be a pre-Devonian event.

The fins of osteichthyans comprise an internal and proximal endoskeletal component (the fin bones) and a distal dermoskeletal component (the fin rays). Polybasal paired fin articulation is assumed to be a primitive gnathostome feature based on its distribution in "placoderms", chondrichthyans, stem sarcopterygians, and actinopterygians. In osteichthyans, the presence of three pterygial radials (i.e., propterygium, mesopterygium and metapterygium) represents the primitive condition (JANVIER 1996), with subsequent loss of the metapterygium in advanced actinopterygians (e.g., teleosts; MABEE, 2000) and loss of the propterygium and mesopterygium in crown sarcopterygians (including tetrapods) that retain only the metapterygium (COATES, 2003; GRANDEL, 2003). The tetrapod limb thus derives from this single pterygial radial and it has been proposed that the subsequent development of bones followed a 'metapterygial axis', although this scenario is greatly debated, especially in reference to the evolution of digits (e.g., SHUBIN & ALBERCH, 1986; COATES, 1995; CLACK, 2009).

Now, dealing with the fin dermoskeleton, it has long been recognized that lepidotrichia, osseous dermal fin rays covering both the paired and unpaired fins (GOODRICH, 1904, Paper IV), are a specialization of osteichthyans (e.g., SCHAEFFER, 1968; ROSEN *et al.*, 1981; GARDINER, 1984; MAISEY, 1986). Proper lepidotrichia (i.e., fully ossified

and articulated dermal fin rays) are absent from the fins of chondrichthyans and most "acanthodians" (see Paper IV for further details). However certain "acanthodians" show partly ossified dermal fin rays and 'lepidotrich-like' scales are present in the fins of some "agnathans" (osteostracans and anaspids; JANVIER, 1996; COATES, 2003), but the latter are considered as convergent with the lepidotrichia of osteichthyans.

### III.3. SARCOPTERYGIAN DIVERSITY

As previously seen, despite a high taxonomical diversity in the Devonian, sarcopterygians are unfortunately represented in the extant nature by only three clades: actinistians (or coelacanths), dipnoans (or lungfishes), and tetrapods. These three groups show very derived morphologies from the primitive sarcopterygian pattern and, moreover, very different between each other.

The main morphological differences between sarcopterygian groups deal with number and position of median fins, endoskeletal elements in the paired fins, and scale morphology. Herein I will present the main groups of sarcopterygians (after JANVIER, 1996) (Fig. III.1.1,2). Each sarcopterygian 'order' will be described on the basis of the best-known members and most generalized forms, when available. Each review will comprise a short introduction about their distribution and phylogenetic interrelationships and an overall description of their fin pattern and squamation (for further information on scales see Paper I, II, III and for postcranial skeleton, fin rays structure, and fin evolution see Paper IV).

### III.3.1. STEM SARCOPTERYGII

The stem sarcopterygians described herein correspond to recently discovered new fossil taxa that cannot be confidently attributed to any of the formerly presented sarcopterygian orders (Fig.III.1.1). These new forms include puzzling fishes from the Late Silurian and Early Devonian of China such as *Psarolepis romeri* YU, 1998*, Achoania jarvikii* ZHU *et al.*, 2001*, Styloichthys changae* ZHU & YU, 2002*, Meemannia eos* ZHU *et al.*, 2006, and *Guiyu oneiros* ZHU *et al.*, 2009. Their phylogenetic position is still debated; *Psarolepis* was formerly considered a dipnomorph (YU, 1998) but now it is generally placed along the stem Sarcopterygii (ZHU *et al.*, 1999, 2001; ZHU & YU, 2002) although LONG (2001) pointed its resemblance with onychodontids. *Styloichthys* was considered the sister group of rhipidistians (ZHU & YU, 2002) but has recently been reconstructed as a putative basal actinistian (FRIEDMAN, 2007a). *Guiyu* could possibly be a basal sarcopterygian (ZHU *et al.*, 2009) but lacks cosmine and show a set of primitive features in its scales that would exclude it from the osteichthyan crown group (FRIEDMAN & BRAZEAU, 2010). *Meemannia* and *Achoania* are generally located as successive sister groups of onychodontids and actinistians along with *Psarolepis* (ZHU *et al.*, 2006).

For most of these early sarcopterygians the postcranial anatomy is still unknown. *Meemannia* and *Achoania* are solely represented by cranial material (ZHU *et al.*, 2001; 2006). *Styloichthys* and *Psarolepis* are known from articulated cranial and disarticulated postcranial material, mostly pectoral girdles (for *Styloichthys*) (ZHU & YU, 2002) and pelvic girdles (for *Psarolepis*) (ZHU *et al.*, 2012a). *Guiyu* is the most completely preserved (QIAO & ZHU, 2010; ZHU *et al.*, 2009, 2012a), and although the caudal fin shape is still hypothetic, the median fin pattern is representative of the primitive condition in osteichthyans, and more particularly in sarcopterygians (Fig. III.4.1.1).

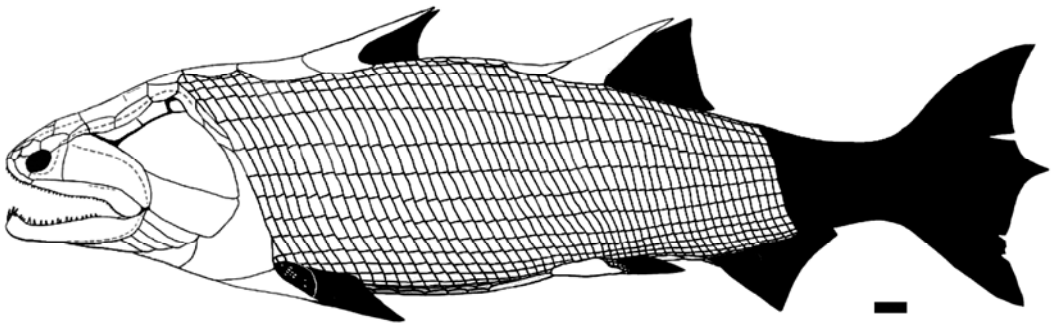


**FIGURE III.3.1.1. Stem Sarcopterygii**. *Guiyu*, the most completely known early osteichthyan as a representative of the overall stem sarcopterygian morphology. Scale bar equals 1 cm. Modified after ZHU *et al.,* 2012a.

The paired fins of *Guiyu* and *Psarolepis* are remarkable in possessing an anterior dermal fin spine, similar to that of Devonian chondrichthyans and "placoderms" (ZHU *et al.*, 2009, 2012a). More dramatically, the pectoral fins of *Psarolepis* and *Achoania* have shown that forms have polybasal pectoral fin articulation as in chondrichthyans and basal actinopterygians (e.g., the articular crest of the scapulocoracoid bears three facets in *Achoania* and four in *Psarolepis*) (ZHU & YU, 2009). Consequently, the origin of the monobasal sarcopterygian fin that only retains the metapterygium must have occurred at a point crownward to *Psarolepis* and *Achoania*, instead of at the separation between sarcopterygians and actinopterygians as previously thought.

*Guiyu* possess two dorsal fins and an anal fin located posteriorly to the second dorsal fin. Both dorsal fins show a bony median fin spine on the trailing edge, as in *Psarolepis* (ZHU *et al.*, 1999). No fin spine is found for the pelvic and anal fins. Lepidotrichia are partially preserved in the pectoral, second dorsal and anal fin of the *Guiyu* holotype (ZHU *et al.*, 2012a). They are segmented and, certainly, covered by enamel.

The scales of the stem sarcopterygians are rhombic in shape and prominently dorso-ventrally elongated (e.g., *Guiyu*, *Psarolepis*, *Styloichthys*) (LU & ZHU, 2008). They are the subject of current intense histological research (QU, *pers. comm*., 2012) due to the combined occurrence of ganoine in *Guiyu* and cosmine-like structures in *Psarolepis*, *Meemannia* and *Styloichthys* (ZHU *et al.*, 2009, 2010).

### III.3.2. ONYCHODONTIDA

The Onychodontida (from the Greek "onukh"=nail or claw and "odontos"=tooth), also known as "Struniiformes" or Onychodontiformes, are an enigmatic basal sarcopterygian clade whose affinities within the Sarcopterygii are disputed (e.g., PANCHEN & SMITHSON, 1987; LONG, 2001; ZHU & SCHULTZE, 2001). Onychodontids were marine predatory fishes of variable size occurring from the Early Devonian (Pragian) to the Late Devonian (Famennian). They are currently represented by six genera: *Bukanodus* JOHANSON *et al.*, 2007; *Grossius* SCHULTZE, 1973; *Lukeus* YOUNG & SCHULTZE, 2005; *Onychodus* NEWBERRY, 1857; *Qingmenodus* LU & ZHU, 2010, and *Strunius* JESSEN, 1966.

It is widely recognized that the Onychodontida are a monophyletic group (CLOUTIER & AHLBERG, 1996; JANVIER, 1996; ANDREWS *et al.*, 2006; CAMPBELL & BARWICK, 2006; *contra* FRIEDMAN, 2007a). For other phylogenetic considerations see SCHULTZE (1987); LONG (1989, 2001); YOUNG *et al.* (1992); CLOUTIER & AHLBERG (1996); ZHU & SCHULTZE (1997, 2001); LU & ZHU (2010) and ZHU *et al.* (1999, 2001, 2006). Morphological descriptions are mostly based on disarticulated and fragmentary skull material. The exoskeleton of the onychodontids is poorly known, except for *Onychodus*

(ANDREWS *et al.*, 2006) and *Strunius* (JESSEN, 1966). The best-known onychodont is *Onychodus* from the Frasnian of Gogo, Western Australia (ANDREWS *et al.*, 2006).

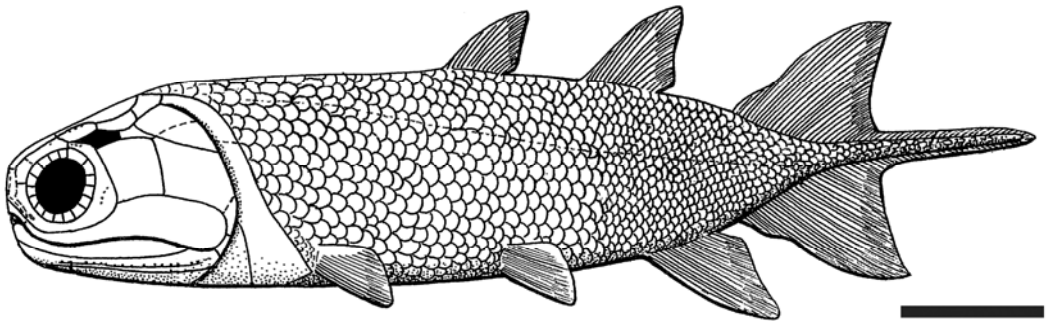


**FIGURE III.3.2.1. Onychodontida**. *Strunius*. Scale bar equals 1 cm. Modified after JESSEN, 1966.

The paired fins of onychodontids are poorly known. They are only preserved in its entirety in *Strunius* where they are small, triangular in shape and of similar size between the pectoral and the pelvic fin (JESSEN, 1966). In *Strunius* the pectoral fin is displaced further back by a posteriorly elongate ventral lamina of the cleithrum and seems to be located more ventrally than in other sarcopterygians. The pelvic fin is located at the level of the first dorsal fin.

The median fin pattern is constant in onychodontids for which fins are preserved and show the classical sarcopterygian condition with two dorsal fins. The caudal fin is diphycercal in *Strunius* and *Onychodus* and shows an elongate median lobe, although in the latter it may extend more dorsally, slightly resembling the heterocercal condition (ANDREWS *et al.*, 2006).

The scales of onychodontids are rounded in shape. They are ornamented with ridges or spoon-shaped tubercles of dentine capped with a thin enamel layer distributed along the entire exposed area of the scale (AQUESBI, 1988). The presence of cosmine was

considered uncertain (JESSEN, 1966) however new discoveries have shown that cosmine is present in the dermal bones of the earliest onychodontid *Qingmenodus* (ZHU & ZHAO, 2005; LU & ZHU, 2010) although the scale shape is still unknown in this taxon.

### III.3.3. ACTINISTIA

The Actinistia, or coelacanths *sensu lato* (from the Greek "koilos"=hollow and "akantha"=spine) are one of the most emblematic groups of lobe-finned fishes. Coelacanths have a long evolutionary history, from the Middle Palaeozoic to Recent, comprising nearly 50 fossil genera (CLOUTIER & FOREY, 1991; FOREY, 1998). Indeed they show a very diverse range of sizes and modes of life ranging from shallow marine and lacustrine environments during the Palaeozoic (CLOUTIER, 1996a) and Mesozoic (POYATO-ARIZA *et al.*, 1998), to deep marine for the extant coelacanth *Latimeria* (FRICKE *et al.*, 1987). They reach their maximum taxonomic diversity during the Lower Triassic (CLOUTIER & FOREY, 1991) however the greatest morphological disparity occurs in the Devonian and the Carboniferous (LUND & LUND, 1985; FRIEDMAN & COATES, 2006).

Our knowledge of early Devonian forms has been greatly enhanced in the past years with the discovery and redescription of some morphologically and phylogenetically important taxa, such as *Shoshonia* (FRIEDMAN *et al.*, 2007), *Holopterygius* (FRIEDMAN & COATES, 2006), *Miguashaia* (CLOUTIER, 1996a), and the putative actinistian *Styloichthys* (ZHU & YU, 2002; FRIEDMAN, 2007a). The extant coelacanth *Latimeria* has given the living landmark from which all descriptions of fossil taxa and comparisons are made (MILLOT & ANTHONY, 1958, 1965, 1978; FOREY, 1998). *Eoactinistia* from the Lower Devonian (Pragian) of Australia is considered as the oldest actinistian (JOHANSON *et al.*, 2006), although it is only known from a dentary bone. *Miguashaia*, a well-preserved and

well-known Late Devonian (Frasnian) actinistian from Québec (CLOUTIER, 1996a) and Latvia (FOREY *et al.*, 2000), is considered as the plesiomorphic sister taxon to all other coelacanths.

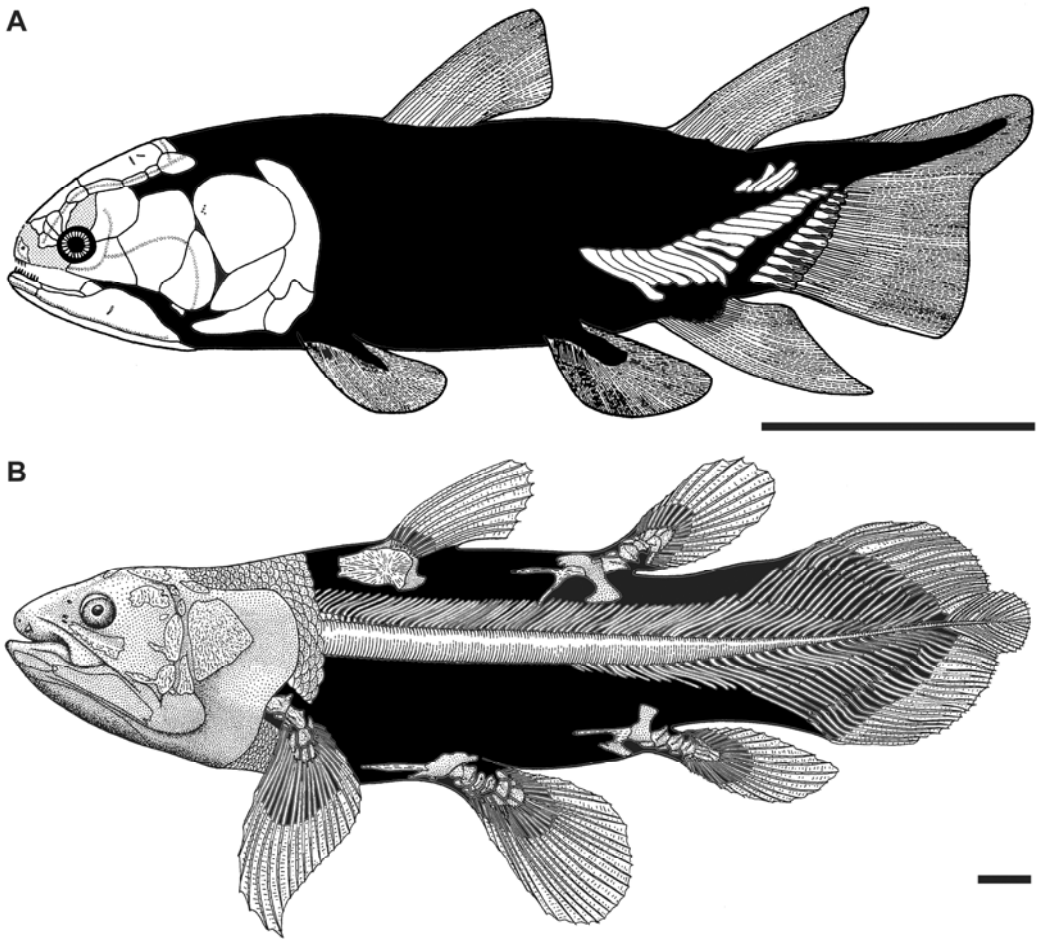



**FIGURE III.3.3.1. Actinistia. A**. *Miguashaia,* as a 'primitive'' coelacanth (modified after CLOUTIER, 1996a), **B.** *Latimeria* as an 'anatomically modern' coelacanth (modified after MILLOT & ANTHONY, 1958; JARVIK, 1980). Scale bars equal 10 cm.

Due to their long evolutionary history and relatively rich fossil record, the amount of data concerning the postcranial and dermal skeleton of actinistians is quite overwhelming among sarcopterygians. The postcranial skeleton of coelacanths is well known and is considered as derived amongst osteichthyans. It used to be described as

conservative in structure throughout the evolutionary history of the group (FOREY, 1998). However, new studies and reassessments of Palaeozoic actinistians (e.g., *Allenypterus, Shoshonia,* and *Holopterygius*) are at odds with this apparent morphological 'stability' (FRIEDMAN & COATES, 2006; FRIEDMAN *et al.*, 2007), showing that early forms present high levels of morphological disparity. The recent discovery of an *Euporosteus* species in the Early Devonian of China has also shown that morphological diversification occurred rapidly at the beginning of Devonian, and has extended the chronological range of what were formerly considered 'derived' or 'anatomically modern' forms (ZHU *et al.*, 2012b) (see below).

The paired fins are single-axis fins (FOREY, 1998). The endoskeleton is composed of four or more large axial mesomeres. In the pectoral fin the endoskeleton is slightly longer than the pelvic fin. The lepidotrichia are arranged around the tip of the fin, with the longest rays being the medial ones. Both the leading preaxial and postaxial lepidotrichia are associated with the radials attached to the fourth mesomeres in *Latimeria* but in some fossil taxa the lepidotrichia can articulate with more proximal mesomeres.

The median fin pattern shows the classical sarcopterygian condition, with two dorsal fins and a characteristic trilobate caudal fin, similar to that of onychodontids, but unique to coelacanths among extant fishes. The anterior dorsal fin is not lobed and is located well anteriorly, usually within the anterior half of the body, a condition different from that of other lobe-finned fishes. The lepidotrichia are supported by a plate-like basal bone strengthened by thickened ridges. The second dorsal fin is also located relatively more anteriorly than in other sarcopterygians and lies opposite, or nearly opposite, to the anal fin. The second dorsal and anal fins are each supported by a single basal plate. In these lobate fins the lepidotrichia articulate with a single axis composed

of a least four endoskeletal mesomeres, which are extremely similar to those forming the axis of the paired fins (FOREY, 1998). As in the paired fins, the lepidotrichia are inserted almost symmetrically around the tip of the fin axis in all lobate median fins.

The caudal fin is composed of three lobes (dorsal, median and ventral lobes) and therefore it is described as trilobate, except in *Allenypterus* (LUND & LUND, 1984, 1985) that posses an asymmetrical tail, and *Miguashaia* (CLOUTIER, 1996a), which has a heterocercal tail. This heterocercal condition characterises the 'primitive' actinistians (*sensu* ZHU *et al.*, 2012b) in contrast to 'anatomically modern' actinistians with the classical trilobated tail (Fig. III.3.3.1).

In most coelacanths, the dorsal (epichordal) and ventral (hypochordal) lobes are approximately equal in size and carry the same number of lepidotrichia, but in many fossil taxa there is a slight asymmetry in the number of caudal lepidotrichia and internal radial supports between the lobes. The dorsal lobe is usually longer than the ventral one; this condition is considered as an apomorphy of coelacanths with trilobate diphycercal fins above *Miguashaia* (CLOUTIER, 1996a).

The supplementary median (or axial) lobe is also a derived feature of coelacanths above *Miguashaia* and it develops as a symmetrical arrangement of fin rays around the terminal end of the notochord. This lobe is always separate from the dorsal and ventral lobes and there is a clear gap between the dermal fin rays of the latter lobes and the fin rays within the median lobe (FOREY, 1998). The precise function of the median lobe remains unknown but it is most probably used during the singular locomotion of coelacanths (FRICKE *et al.*, 1987). MILLOT and ANTHONY (1958) postulated that it could be able to regenerate in *Latimeria*.

The scales of actinistians are rounded in shape. They are ornamented with horseshoe-shaped tubercles (as in onychodontids) and/or with coarse or thin dentine-made ridges capped with enamel in certain taxa (e.g., *Latimeria*); this ornamentation pattern is uniformly maintained in all actinistians from the Palaeozoic to Recent. Cosmine is present in the rhombic scales of the putative basal actinistian *Styloichthys* (ZHU *et al.*, 2002; FRIEDMAN, 2007a; LU & ZHU, 2008). *Miguashaia*, the most 'primitive' actinistian do not possess cosmine and shows rounded scales with the classical ornamentation formerly described (CLOUTIER, 1996a).

### III.3.4. DIPNOMORPHA

The Dipnomorpha comprise all taxa more related to lungfishes than to tetrapods; (i.e. the Dipnoi and their sister group the Porolepiformes). The taxon Dipnomorpha was erected by AHLBERG (1991) and has proven to be a well-sustained and clade in all phylogenetic analyses of sarcopterygians.

Besides the well-defined clades of the Porolepiformes and the Dipnoi, three uncertainly located taxa are gathered among the Dipnomorpha. *Powichthys* from the lower Early Devonian of Canada and Spitsbergen (JESSEN, 1975; CLÉMENT & JANVIER, 2004) was interpreted as the sister taxon of dipnoans and close relatives by AHLBERG (1991), CLOUTIER and AHLBERG (1996), and ZHU *et al.* (2001). FOREY (1998) considered it as the sister taxon of all other Dipnomorpha, whereas ZHU & SCHULTZE (1997, 2001) considered it as the sister taxon of all other Sarcopterygii except *Youngolepis*, *Diabolepis*, and the Dipnoi. *Powichthys* is currently considered to be closer to porolepiforms than to dipnoans (CLÉMENT & JANVIER, 2004; CLÉMENT & AHLBERG, 2010).

*Youngolepis* from the Early Devonian of China (CHANG & YU, 1981; CHANG, 1982) was described as a stem dipnoan and, along with *Diabolepis* they would represent two progressive sister groups of the Dipnoi. However, CHANG and SMITH (1992) put both *Youngolepis* and *Powichthys* nearer to porolepiforms than to dipnoans. A new Chinese form *Arquatichthys porosus* from the Pragian (LU & ZHU, 2008) has been considered a stem dipnomorph, although with caution. In summary, we can say that these forms show a series of generalized sarcopterygian and dipnomorph features that complicate their phylogenetic placement.

#### III.3.4.1. POROLEPIFORMES

The Porolepiformes (from the Greek "poros"=pore and "lepidos"=scale) are an exclusively fossil group of predatory sarcopterygians that inhabited near-shore marine and lacustrine environments from the Early Devonian (Lochkovian) to the latest Devonian (Famennian). Currently, the Porolepiformes comprise 12 genera: *Duffichthys* AHLBERG, 1992; *Glyptolepis* MILLER ex AGASSIZ, 1841; *Hamodus* OBRUCHEV, 1933; *Heimenia* ØRVIG, 1969; *Holoptychius* AGASSIZ, 1839; *Laccognathus* GROSS, 1941; *Nasogaluakus* SCHULTZE, 2000; *Paraglyptolepis* VOROBYEVA, 1987; *Porolepis* WOODWARD, 1891; *Pseudosauripterus* BALL *et al.*, 1961; *Quebecius* SCHULTZE, 1973; and *Ventalepis* SCHULTZE, 1980.

JARVIK (1942) split the order Porolepiformes in two families: Porolepididae (comprising *Porolepis* and *Heimenia*) from the Early and Middle Devonian, and Holoptychiidae (comprising *Holoptychius*, *Glyptolepis* and *Laccognathus,* among others) from the Middle and Late Devonian. There is little morphological variation between both families; the "porolepidids" differ from the holoptychiids in having a longer anterior

cranial division, a posteriorly shallow lower jaw, and a cosmine covering on their rhombic scales and dermal bones (AHLBERG, 1992b), whereas holoptychiids present rounded scales devoid of cosmine (ØRVIG, 1957). The best-known genera are *Porolepis* (JARVIK, 1942; CLÉMENT, 2004), *Heimenia* (CLÉMENT, 2001a,b; Paper I), *Glyptolepis* (ANDREWS & WESTOLL, 1970b; JARVIK, 1972), *Holoptychius* (ANDREWS & WESTOLL, 1970b; CLOUTIER & SCHULTZE, 1996), and *Quebecius* (SCHULTZE & ARSENAULT, 1987; CLOUTIER & SCHULTZE, 1996) in which the postcranial and fin skeleton are well preserved.

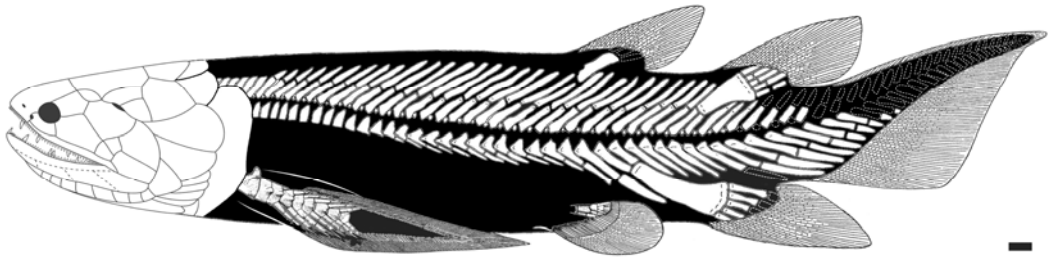


**FIGURE III.3.4.1.1. Porolepiformes**. *Glyptolepis*. Scale bar equals 1 cm. Redrawn and modified after ANDREWS & WESTOLL, 1970b; JARVIK, 1972; AHLBERG, 1989, 1991.

The monophyly of the group has been well established (CLOUTIER & AHLBERG, 1996), however "Porolepididae" is defined mainly on plesiomorphic characters for sarcopterygians and therefore it could be considered as a paraphyletic assemblage of primitive porolepiforms (MAISEY, 1986; AHLBERG, 1991; 1992a,b, CLÉMENT, 2001b). However very few studies have tackled the precise phylogenetic relationships within the group (e.g., SCHULTZE, 2000; CLÉMENT, 2001b). *Porolepis* is the sister group of all other Porolepiformes.

The paired fins of porolepiforms tend to differ in shape and size between the pectoral and the pelvic fins. The pectoral fins are long, leaf-like, nearly symmetrical, and

usually narrow, with an elongate lobed middle region in all known taxa. The pelvic fins are short, asymmetrical, usually rounded and lobate, except in *Quebecius* that shows broadly based pelvic fins (SCHULTZE & ARSENAULT, 1987; CLOUTIER & SCHULTZE, 1996). They are smaller than the pectoral fins and are located in the middle region of the body, anterior to the first dorsal fin. As in the leaf-like fins of dipnoans and actinistians, the lepidotrichia articulate with the radials on both preaxial and postaxial sides of the fins.

The median fin pattern, as that in other lobe-finned fishes, shows two similarly-shaped dorsal fins located in the posterior half of the body. The first dorsal fin is always slightly smaller than the second one. The second dorsal fin is usually located opposite or somewhat posteriorly to the anal fin and equal in size with the latter. Between the genera for which postcranial and fin material is known, the main morphological differences among the dorsal fins concern the lobation of the proximal region; they are lobate in *Porolepis* (CLÉMENT, 2004), *Holoptychius* (CLOUTIER & SCHULTZE, 1996), and *Glyptolepis* (ANDREWS & WESTOLL, 1970b; AHLBERG, 1989), whereas *Quebecius* shows a singular dorsal, anal and pelvic fin shape with broad insertion fields (SCHULTZE & ARSENAULT, 1987; CLOUTIER & SCHULTZE, 1996) similar to that of *Onychodus*.

The caudal fin is heterocercal in all known porolepiforms and presents a well developed hypochordal lobe and a small epichordal lobe, except in *Porolepis* where the epichordal lobe is absent (CLÉMENT, 2004). The posterior margin of the hypochordal lobe is almost straight in *Porolepis* (Paper IV, fig.4) but more rounded and sigmoid in holoptychiids (CLOUTIER & SCHULTZE, 1996; CLÉMENT, 2004). In *Porolepis* (CLÉMENT, 2004), *Holoptychius* and *Quebecius* (CLOUTIER & SCHULTZE, 1996), the fin rays of the ventral lobe of the caudal fin diminish in size from anterior to posterior. The same is true for the dorsal lobe in *Holoptychius* and *Quebecius*.

The scales of porolepiforms are morphologically and histologically variable. In "porolepidids" the squamation is composed of thick rhombic scales covered with cosmine (e.g., *Porolepis*) whereas in holoptychiids the scales are thin, rounded, and lack cosmine (e.g., *Holoptychius*). These characters used to be considered as mutually exclusive and characteristic of the two families within the Porolepiformes. The rhombic scales of "porolepidids" possess the characteristic peg and socket articulation and an oblique articular ridge (or keel) in the internal surface. In holoptychiids the keel and the peg-and-socket articulation are lost, associated with the acquisition of a rounded shape of the scales. The condition of *Heimenia* is informative on the evolutionary transformation of the squamation between "porolepidids" and holoptychiids (Paper I).

#### III.3.4.2. DIPNOI

The Dipnoi (from the Greek "dis"=double and "pnoe"=breathing), generally known as lungfishes or dipnoans, are a diverse group of sarcopterygians with a long and well-documented fossil record extending from the Early Devonian (Pragian) to Recent. Dipnoans are diagnosed by a complicated cranial architecture (CLOUTIER & AHLBERG, 1996). They are also best characterized by their large tooth plates derived from palatal bones (JANVIER, 1996). There are more than 70 described fossil genera known mostly from disarticulated tooth plates. They reached their maximum diversity during the Devonian and Triassic (SCHULTZE, 2004). Today they are represented by three extant genera: *Protopterus* (four species, *P. dolloi, P. annectens, P. aethiopicus,* and *P. amphibius)* from equatorial Africa, *Lepidosiren* (one species, *L. paradoxa)* from South America, and *Neoceratodus* (one species, *N. forsteri)* from Australia (KEMP, 1986).

The oldest known members of the Dipnoi are *Uranolophus wyomingensis* from Wyoming, USA (DENISON, 1968a,b) and *Speonesydrion iani* from New South Wales, Australia (CAMPBELL & BARWICK, 1983) from the Pragian (Early Devonian). Other early dipnoans are *Sorbitorhynchus deleaskitus* (WANG *et al.,* 1990) and *Dipnorhynchus suessmilchi* (ETHERIDGE, 1906) from the Emsian of China and Australia, respectively. MILES (1977) described *Uranolophus* as the most basal dipnoan, however CAMPBELL and BARWICK (1987) considered it more derived than *Speonesydrion* and *Dipnorhynchus. Diabolepis speratus* (CHANG & YU, 1984) from the Pragian of Yunnan (China) is considered as the sister group of all other dipnoans (CAMPBELL & BARWICK, 2001).

The monophyly of the Dipnoi has been well demonstrated; however, since the discovery of *Diabolepis* (CHANG & YU, 1984) the definition and diagnostic features of the group have been debated and reformulated (MAISEY, 1986; CAMPBELL & BARWICK, 1987; PANCHEN & SMITHSON, 1987; SCHULTZE, 1987; SCHULTZE & CAMPBELL, 1986; CLOUTIER, 1990; SMITH & CHANG, 1990; CHANG, 1991a). Interrelationships among dipnoans have been assessed in several studies but remain highly debated (MILES, 1977; MARSHALL, 1987; CAMPBELL & BARWICK, 1990, 2001; SCHULTZE & MARSHALL, 1993; LONG, 1993; FRIEDMAN, 2007b). Attempts of classification have been made based on dentition (i.e., tooth-plated, dentine-plated, and denticulated dipnoans) (CAMPBELL & BARWICK, 1983, 1987, 1990; AHLBERG *et al*., 2000) but currently there is no global consensus concerning the phylogeny of the group.

Unfortunately, early dipnomorphs such as *Diabolepis, Youngolepis* and *Powichthys* are of little use for comparisons on the postcranial skeleton of dipnoans they are known exclusively from cranial material (JESSEN, 1980; CHANG & YU, 1984; CHANG, 1991b; CLÉMENT & JANVIER, 2004) and isolated dentitional elements (SMITH & CHANG, 1990; CHANG & SMITH, 1992). The oldest proper dipnoan, *Uranolophus* is known from a single

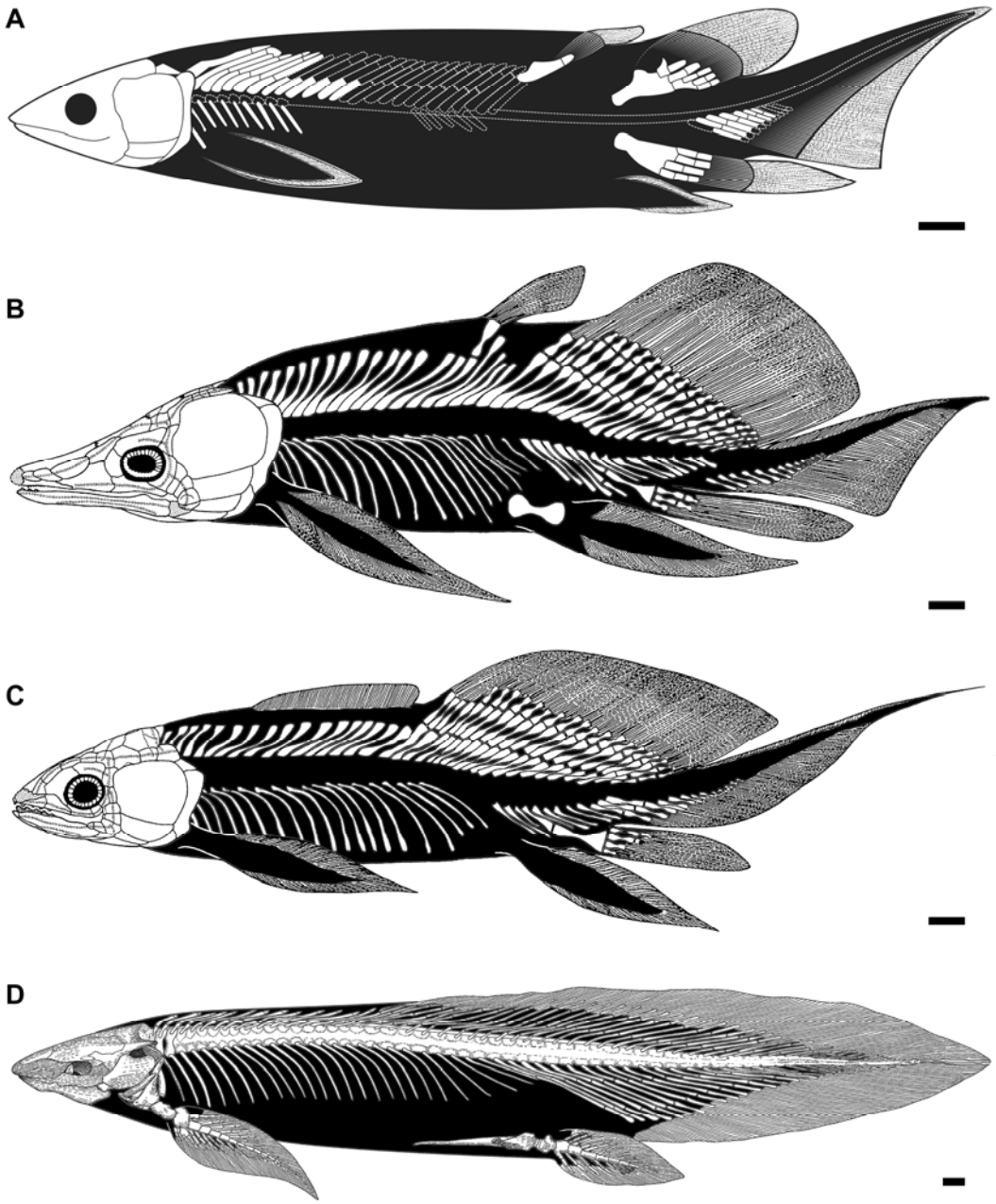



**FIGURE III.3.4.2.1. Dipnoi**. **A.** *Dipterus* (redrawn and modified after AHLBERG & TREWIN, 1995), **B.** *Fleurantia* (modified after CLOUTIER, 1996b), **C.** *Scaumenacia* (modified after CLOUTIER, 1996b), **D.** *Neoceratodus* (modified after JARVIK, 1980). Scale bars equal 1 cm.

complete specimen and numerous skulls and lower jaws (DENISON, 1968a,b; CAMPBELL & BARWICK, 1988) and allows setting the primitive pattern for the postcranial skeleton in dipnoans. *Dipterus valenciennesi* from the Eifelian-Givetian (Middle Devonian) of

Scotland is the best-known representative of the early dipnoans, being known from whole bodies with well-preserved cranial and postcranial endoskeleton (AHLBERG & TREWIN, 1995).

The postcranial skeleton of early dipnoans like *Uranolophus* or *Dipterus* deviates slightly from the generalized sarcopterygian condition and dramatically resembles that of porolepiforms (DENISON, 1968a; CAMPBELL & BARWICK, 1988; AHLBERG, 1989, 1991, 1992b; AHLBERG & TREWIN, 1995) (Fig. III.3.4.2.1). However, during the Middle to Late Devonian, new morphologies arose deriving from the primitive pattern (AHLBERG & TREWIN, 1995; CLOUTIER, 1996b). As FRIEDMAN (2010) pointed out, postcranial anatomy can be a potential source of new characters that would help to elucidate their controversial phylogenetic interrelationships.

Paired fins of dipnoans are highly conservative in shape throughout most of their evolutionary history. The paired and pectoral fins are mirror images of each other, with the pelvic fin being always slightly smaller than the pectoral one. They are long, leaf-like, nearly symmetrical, and usually narrow fins, with an elongate lobed middle region, very similar to that of porolepiforms. The only exceptions are the paired fins of the extant *Lepidosiren* and *Protopterus* that show small, thin and filament-like paired fins with reduced fin rays.

The median fins morphology is highly variable in dipnoans, especially in the early forms from the Devonian and Carboniferous. The median fin pattern can be divided into five broad morphotypes regarding the arrangement of the endoskeleton elements in the fins (for a more detailed classification based on dorsal fin endoskeleton see FRIEDMAN, 2010) (Fig. III.3.4.2.2).

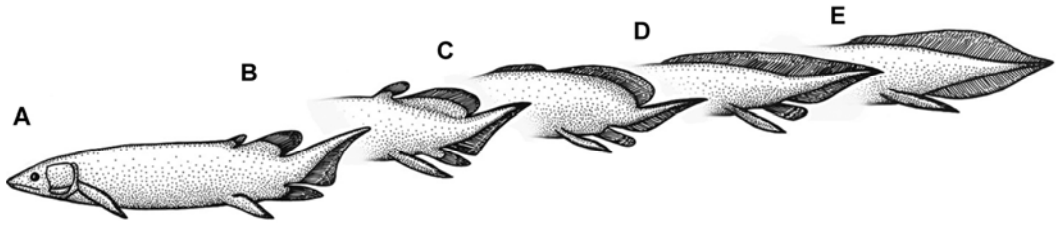



**FIGURE III.3.4.2.2. Evolutionary transformation of the median fins in the dipnoans.** The median fin pattern can be divided into five broad morphotypes; **A.** Independent short-based median fins, heterocercal caudal fin (e.g., *Dipterus*). **B.** Independent short-based first dorsal and anal fin, long-based second dorsal fin, heterocercal caudal fin (e.g., *Fleurantia*); **C.** Independent long-based dorsal fins, short-based anal fin, heterocercal caudal fin (e.g., *Scaumenacia*); **D.** Dorsal fins incorporated into the caudal fin forming a diphycercal fin fringe with a separated short-based anal fin (e.g., *Phaneropleuron*); **E.** Loss of the anal fin, dorsal and caudal fin incorporated in a continuous diphycercal fin fringe (e.g., *Neoceratodus*). Not to scale. Modified after CLOUTIER, 2010.

The scales of dipnoans are also variable in shape and microstructure. The earliest forms show rhombic (e.g., *Uranolophus*) or rounded scales (e.g., *Dipterus*) with patches or a continuous cosmine covering. The dipnoan cosmine is characterized by the presence of more or less concentric lines of discontinuity in the enamel, the so-called Westoll lines, which are interpreted as being due to cyclic resorption and redeposition during growth (Ørvig, 1969a) and are a distinctive feature of this group. From the Late Devonian onwards, lungfishes show a tendency towards bone reduction (in the endo- as well as in the dermoskeleton) and loss of the cosmine in their rounded scales. The extant forms (e.g., *Neoceratodus*) show rounded scales ornamented with fine, slightly undulating bony ridges.

### III.3.5. TETRAPODOMORPHA

The Tetrapodomorpha comprise all taxa more related to tetrapods than to dipnoans (i.e., rhizodontids, "osteolepiforms", "elpistostegalians" and tetrapods). The taxon was erected by AHLBERG (1991), along with Dipnomorpha, and, as with the latter, the group has proven to be a well-sustained clade in all phylogenetic analysis on sarcopterygians.

Tetrapodomorpha and Dipnomorpha form the clade Rhipidistia. This taxon was formerly defined on the basis of plicidentine only (AHLBERG, 1991; JANVIER, 1996) (for further information see Paper II) but the presence of folded dentine in *Psarolepis* (ZHU *et al.*, 1999) makes this character no longer reliable for rhipidistians. Plicidentine is also secondarily absent from dipnoans (e.g., *Diabolepis*, SMITH & CHANG, 1990)

Tetrapodomorphs show significant anatomical modifications of the nasal region and anterior palate (e.g., the appearance of the choanae) as well as the pectoral appendages (e.g., the differentiation of a robust zeugopod formed by two bones: the radius and ulna in the pectoral fin, and the tibia and fibula in the pelvic fin), among other characters. The recognition of 'tetrapod-like' features in fossil sarcopterygian fishes attest that most of the characters that are commonly linked to terrestrial vertebrates evolved in fishes during the Devonian.

*Kenichthys campbelli* from the Emsian (Middle Devonian) of China (CHANG & ZHU, 1993) is the earliest representative of the Tetrapodormorpha and the sister group of all other tetrapodomorphs. *Kenichthys* is known by well-preserved skull and pectoral girdle material (CHANG & ZHU, 1993; ZHU & AHLBERG, 2004). Thorough study of the skull bones showed that the tetrapod choanae were indeed posterior nostrils displaced into the palate, in the same way as in lungfishes, although their position in the palate is not

homologous (JANVIER, 2004). *Kenichthys* possess cosmine on its dermal bones and scales. The scales are rhombic in shape, and very similar to that of rhombic-scaled "osteolepiforms", with a marked antero-dorsal groove between the overlapped and exposed surfaces. Unfortunately, the postcranial skeleton is unknown.

#### III.3.5.1. RHIZODONTIDA

The Rhizodontida (from the Greek "rhiza"=rooth and "odontos"=tooth) are a puzzling group of lobe-finned fishes that play a key role in our understanding of the radiation of tetrapodomorphs during the Devonian. Certain rhizodontids were very large predatory fishes (e.g., *Rhizodus hibberti* from the Lower Carboniferous of Scotland could reach up to 7 m in lenght) (ANDREWS, 1973) that inhabited in marine to fresh water environments from the Middle-Late Devonian (Frasnian) to the Late Carboniferous (Westphalian). They are currently represented by nine genera: *Archichthys* HANCOCK & ATHEY, 1870; *Aztekia* JOHANSON & AHLBERG, 2001; *Barameda* LONG, 1989; *Gooloogongia* JOHANSON & AHLBERG, 1998; *Letognathus* BRAZEAU, 2005; *Rhizodus* OWEN, 1840; *Sauripterus* HALL, 1843; *Screbinodus* ANDREWS, 1985; and *Strepsodus* HUXLEY & ETHERIDGE 1865.

The order Rhizodontida is considered monophyletic (YOUNG *et al.*, 1982; LONG, 1989; JOHANSON & AHLBERG, 2001); however their phylogenetic position amongst the Tetrapodomorpha is still debated (LONG, 1985, 1989; VOROBYEVA & SCHULTZE, 1991). Within the Rhizodontida, *Gooloogongia* is considered as the sister group of all other rhizodontids (JOHANSON & AHLBERG, 2001).

The postcranial skeleton of rhizodontids is poorly known. The best-known rhizodontids are *Strepsodus anculonamensis* (ANDREWS, 1985) from the Carboniferous of

Scotland and *Gooloogongia loomesi* (JOHANSON & AHLBERG, 2001) from the Late Devonian of Australia for which several postcranial elements have been described. Formerly represented merely by pectoral fin remains, *Sauripterus* is now known by several juvenile, nearly complete specimens (GREGORY, 1935; DAVIS *et al.*, 2001, 2004) from the Late Devonian of USA. The type material of *Strepsodus anculonamensis* could also belong to a juvenile (ANDREWS, 1985).

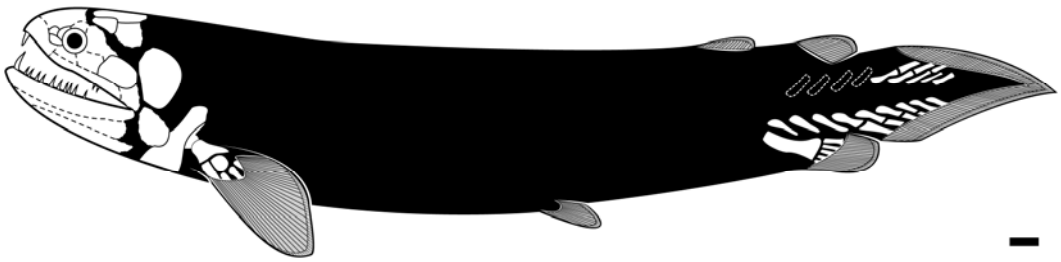


**FIGURE III.3.5.1.1. Rhizodontida**. *Strepsodus*. Scale bar equals 1 cm. Redrawn and modified after ANDREWS, 1985.

In rhizodontids, the paired fins differ in size and shape. The pectoral fins are greatly enlarged and form prominent paddles (GARVEY *et al*., 2005; HOLLAND *et al*., 2007). The pelvic fins are always small, compared to the enlarged pectoral fins, and are located midway of the trunk in *Strepsodus* (ANDREWS, 1985) (Fig. III.3.5.1.1) or more posteriorly, at the level of the second dorsal fin, in *Gooloogongia* (JOHANSON & AHLBERG, 2001).

The median fin pattern shows the classical sarcopterygian condition, but also with remarkable differences in shape and size between the fins. There are two small dorsal fins, located in the posterior half of the body, arranged close together, and near the caudal fin. In *Strepsodus* (ANDREWS, 1985) the anal fin is located slightly behind the level of the second dorsal fin, whereas in *Gooloogongia* (JOHANSON & AHLBERG, 2001) the

anal fin seems to lie anteriorly to the second dorsal fin. In all rhizodontids, the anal, first and second dorsal fins are usually small and show a rounded to slightly pointed outline.

The caudal fin shape is also variable; it can be heterocercal, as in *Gooloogongia* (JOHANSON & AHLBERG, 2001), or diphycercal, as in *Strepsodus* (ANDREWS, 1985), and probably in *Sauripterus* (DAVIS *et al.*, 2001). The heterocercal caudal fin of *Gooloogongia* is composed of two well developed epichordal and hypochordal lobes unequal in size, the epichordal lobe being smaller than the hypochordal one, a condition very common among sarcopterygians, but not as reduced as that of holoptychiids or "osteolepidids" (JARVIK, 1980). The diphycercal caudal fins of *Strepsodus* and *Sauripterus* show a rather thick axial peduncle and are posteriorly elongate with symmetrical dorsal and ventral lobes, resembling the diphycercal tail of dipnoans and Devonian tetrapods.

The scales of rhizodontids are rounded in shape, with a pointed posterior end in certain taxa (e.g., *Gooloogongia*). They are ornamented with fine bony ridges. Cosmine is unknown in all known rhizodontids, despite its presence in *Kenichthys* (CHANG & ZHU, 1993). However, new redescriptions of uncertainly placed "osteolepiforms" that can be revealed to be rhizodontids (COATES & FRIEDMAN, 2010), could show evidence of cosmine in primitive members of the Rhizodontida (see Discussion). The internal surface is smooth and bears a central drop-shaped boss, identical to that of tristichopterids.

#### III.3.5.2. "OSTEOLEPIFORMES"

The "Osteolepiformes" (from the Greek "osteon"=bone and "lepidos"=scale) are a diverse paraphyletic assemblage of Palaeozoic sarcopterygians consisting of small to large predatory fishes from marine and fresh water environments. Almost 50 genera of "osteolepiforms" are known but, despite their large radiation during the Devonian, they

show a rather conservative gross morphology. "Osteolepiforms" are known from the Middle Devonian (Eifelian) (CLOUTIER, 1996c), to the Lower Permian (Sakmarian) (SCHULTZE & HEIDTKE, 1986).

The stretch of lobe-finned fishes considered as "osteolepiforms" has varied between studies during the last years; Osteolepiformes used to include all taxa more related to tetrapods than to lungfishes (i.e. the current definition of Tetrapodomorpha). However today the "osteolepiform" assemblage comprises all extinct sarcopterygian tetrapodomorphs falling between rhizodontids and *Panderichthys* (Fig. III.1.1, 2).

The "Osteolepiformes" have been traditionally subdivided in two groups: the primitive "Osteolepididae", characterized by rhombic scales covered with cosmine, and the more derived, closer to tetrapods, Tristichopteridae (or disused Eusthenopteridae), characterized by rounded scales lacking cosmine. New phylogenetic studies have changed this vision and today the paraphyletic assemblage of the "Osteolepiformes" has been split in several monophyletic families of generalized appearance such as Megalichthyidae, Canowindridae and Tristichopteridae, and some paraphyletic, uncertainly located, "Osteolepididae" such as *Gogonasus*, *Litoptychus, Medoevia*, *Osteolepis*, and *Gyroptychius*, among others (e.g., AHLBERG & JOHANSON, 1998; SNITTING, 2008a,b).

"Osteolepiforms" are central in our knowledge of the 'fish-tetrapod transition'. Many characters evolved in parallel in derived "osteolepiforms" and in tetrapods towards a morphology of large predatory fishes, and some of the main morphological transformations related to the origin of tetrapods took place in the crownward section of the Tetrapodomorpha (i.e., "osteolepiforms" and, most particularly, tristichopterids). Despite the fact that "Osteolepiformes" is of no longer formal taxonomic value, I will use the term throughout this thesis to gather these taxa located between rhizodontids and

"elpistostegalians" in an easily discernible assemblage, knowing that the group is actually considered a grade (AHLBERG & JOHANSON, 1998).

The postcranial skeleton of "osteolepiforms" is one of the best known among fossil fishes thank to the numerous works of JARVIK on the tristichopterid *Eusthenopteron foordi*, the most thoroughly studied and best known fossil vertebrate (see JARVIK, 1980 and references therein). Relatively complete postcranial material is also known for *Osteolepis* (JARVIK, 1948), *Canowindra* (THOMSON, 1973), *Latvius* (JESSEN, 1973), *Gyroptychius* (JARVIK, 1985), *Cladarosymblema* (FOX *et al.*, 1995), *Cabonnichthys* (AHLBERG & JOHANSON, 1997), *Mandageria* (JOHANSON & AHLBERG, 1998), *Heddleichthys* (SNITTING, 2009), and *Askerichthys* (BORGEN, 2011).

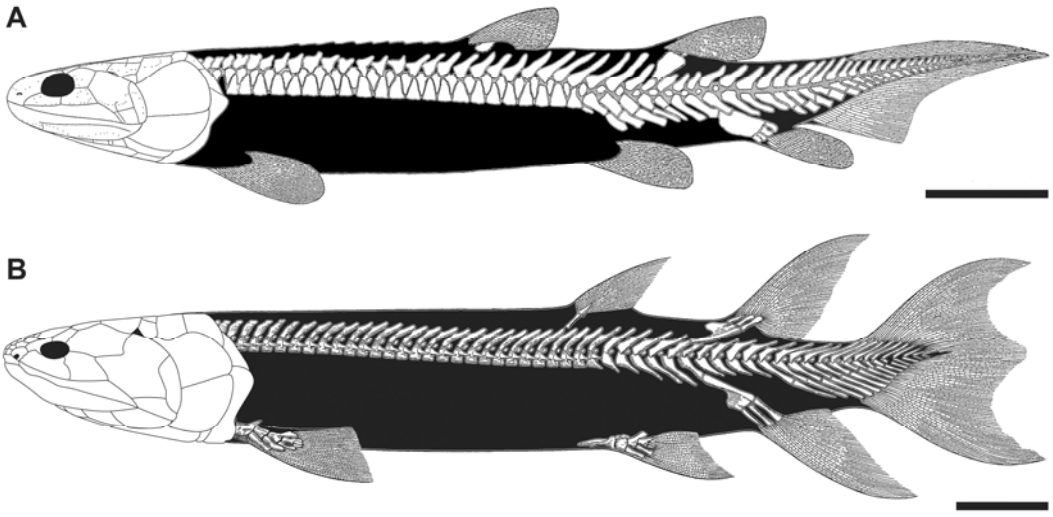



**FIGURE III.3.5.2.1. "Osteolepiformes"**. **A.** *Osteolepis*, an ''osteolepidid'' (modified after JARVIK, 1980, 1985), scale bar equals 1 cm ; **B.** *Eusthenopteron*, a tristichopterid (redrawn and modified after JARVIK, 1980), scale bar equals 10 cm.

The paired fins are rather conservative in structure and morphology among "osteolepiforms". In "osteolepidids" like *Osteolepis* and *Gyroptychius* they are rounded in overall shape (JARVIK, 1985), whereas in tristichopterids, such as *Eusthenopteron* they

are more triangular and posteriorly pointed (JARVIK, 1980). The pelvic fins are slightly smaller than the pectoral ones and are usually located posteriorly, either at the level of the first dorsal fin (e.g., *Gyroptychius, Eusthenopteron*), or between the first and dorsal fins (e.g., *Osteolepis, Glyptopomus*) (JARVIK, 1950).

The median fin pattern is highly conservative in the group; the differences between taxa rest mainly in the proportions of the body and fins. As in other sarcopterygians there are two posteriorly located dorsal fins, with the anterior dorsal fin being always smaller than the posterior one. The anal fin is of similar size as the second dorsal fin and lies opposite or slightly posterior to the latter in the ventral region.

The well-developed caudal fin can be heterocercal (e.g., *Osteolepis*) or diphycercal (e.g., *Gyroptychius* and tristichopterids). There is a great diversity in the diphycercal caudal fin morphology in "osteolepiforms" where it represents the derived condition. For instance in *Eusthenopteron* (JARVIK, 1952) the enlargement of the median axial lobe gives to the diphycercal caudal fin a trilobate shape. In *Gyroptychius* (JARVIK, 1985) the epi- and hypochordal lobes are almost symmetrical, whereas in *Askerichthys* (BORGEN, 2011) and *Tristichopterus* (JOHANSON & AHLBERG, 2001, *pers. obs.*), the hypochordal lobe is larger than the epichordal one. A symmetrical caudal fin in *Gyroptychius* and tristichopterids is also present in more derived tetrapodomorphs (i.e., "elpistostegalians" and tetrapods, see below) and constitutes a general trend in tetrapodomorph evolution.

The scales of "osteolepiforms" vary in size, shape, and microstructure. "Osteolepidids" (e.g., Megalichthyidae, *Osteolepis*, *Gyroptychius*, etc.) possess cosmine-covered rhombic scales with a well-developed peg and socket articulation and an internal articular ridge, whereas certain derived forms (e.g., *Canowindra*;

tristichopterids) show rounded scales lacking cosmine in which the articular ridge has been transformed into a characteristic drop-shaped boss in the internal surface. The rhombic scales of "osteolepidids" differ from other rhombic scales (e.g., porolepiforms) by the presence of well-marked groove that separates the overlapped and exposed areas, as in *Kenichthys,* and a different density and size of the cosmine pores. Rounded scales of tristichopterids are ornamented with fin bony ridges, as in rhizodontids, (JARVIK, 1980; ZYLBERBERG *et al.*, 2010) whereas in *Canowindra* they show a series of small tubercles (THOMSON, 1973).

#### III.3.5.3. "ELPISTOSTEGALIA"

"Elpistostegalia" (from the Greek "elpisto"=hoped-for and "stego"=covered or protected by a roof) or "Panderichthyida" are the closest fossil relatives to tetrapods. They were large predatory fishes inhabiting the shallow waters of deltas and estuaries from Euramerica and occurring exclusively during the Late Devonian (Frasnian). Three genera are currently known: *Elpistostege* from Miguasha, Québec (WESTOLL, 1938; SCHULTZE & ARSENAULT, 1985; SCHULTZE, 1996a); *Panderichthys* from Latvia and Russia (VOROBYEVA & LYARSKAYA, 1968), and *Tiktaalik* from the Ellesmere Island in the Canadian Arctic (DAESCHLER *et al.*, 2006).

"Elpistostegalia" currently constitute a grade of crownward tetrapodomorphs, different from "osteolepiforms", and are situated immediately below tetrapods (Fig. III.1.1). However the name can also be used for the node along the tetrapod stem lineage that includes the common ancestor of *Tiktaalik*, *Panderichthys*, *Elpistostege* and tetrapods (DAESCHLER *et al.*, 2006). Here I will refer to this paraphyletic assemblage of

finned tetrapodomorphs located at the tetrapod stem as “elpistostegalians” rather than “elpistostegalian fishes”.

“Elpistostegalians” share numerous features with Devonian tetrapods such as a long flattened skull with dorsally located eyes, the presence of ribs and the loss of the anterior dorsal fins, among other traits. However, they also retain primitive tetrapodomorph features such as a rhombic scale covering and paired fins with lepidotrichia (DAESCHLER *et al.*, 2006). *Panderichthys* and *Tiktaalik* are known from relatively complete and well preserved postcranial material (VOROBYEVA, 1980; DAESCHLER *et al.*, 2006) whereas *Elpistostege* is solely known by an incomplete skull and several disarticulated vertebrae (SCHULTZE, 1996a). *Panderichthys* seem to be the most basal “elpistostegalian”. *Tiktaalik* is the best-preserved and best-known “elpistostegalian” despite the absence of the caudal fin (Fig. III.3.5.3.1).


**FIGURE III.3.5.3.1 “Elpistostegalia”**. **A.** *Panderichthys* (modified after BENTON, 2005), **B.** *Tiktaalik* (redrawn and modified after DAESCHLER *et al.*, 2006). Scale bars equal 10 cm.

The paired fins of "elpistostegalians" differ from those of other finned tetrapodomorphs in having an expanded endoskeleton and a relatively reduced dermal fin web (BOISVERT, 2005; BOISVERT *et al*., 2008). In *Panderichthys* and *Tiktaalik* pectoral and pelvic fins are located in an extreme ventral position (VOROBYEVA & SCHULTZE, 1991). The pectoral fins are relatively stouter than in other tetrapodomorphs (SHUBIN *et al.*, 2006). The pelvic fins are usually much smaller than the pectoral ones and lie well posteriorly, next to the caudal fin, occupying the level of the anal fin in other sarcopterygians (e.g., "osteolepiforms"). The fin web is leaf-like and distally pointed.

The median fins are exclusively represented by the caudal fin; anal and dorsal fins are absent. In *Panderichthys*, the tail is diphycercal and posteriorly pointed with two symmetrical dorsal and ventral lobes, very similar to that of derived "osteolepiforms" and early tetrapods. The dorsal lobe extends more anteriorly than the ventral one.

The scales of "elpistostegalians" are rhombic in shape, but do not possess cosmine. They are ornamented by a series of bony coarse tubercles. They show the classical rhombic condition with a well-developed 'peg-and-socket' articulation and an internal keel, as in "porolepidids" and "osteolepidids" (see Paper III for further details).

#### III.3.5.4. TETRAPODA

Tetrapoda (from the Greek "tetra"=four and "podos"=foot) is a monophyletic group comprising all limbed vertebrates, from amphibians and reptiles to birds and mammals. Tetrapods are diagnosed by the possession of four limbs with digits, as opposed to fins with fin rays. Tetrapods are highly diverse (with around 30.000 extant species and probably more than twice as many fossil species) and occupy all kinds of habitats, from the deep seas to the airs, and from desserts to polar ice sheets (LECOINTRE

& LE GUYADER, 2001). Such ecological diversity has been achieved thank to the great plasticity and adaptability of the tetrapod limb responsible for the wings of bats and birds, the legs of horses, and the flippers of dolphins. The number of digits per limb is highly variable depending on the group and shows a progressive reduction from an original polydactylous condition in Devonian forms (COATES & CLACK, 1990; CLACK, 2002c; CLACK & FINNEY, 2005). Anterior, posterior, or both sets of limbs can disappear in certain groups such as cetaceans (disappearance of the hind limbs), snakes and caecilians (disappearance of all limbs).

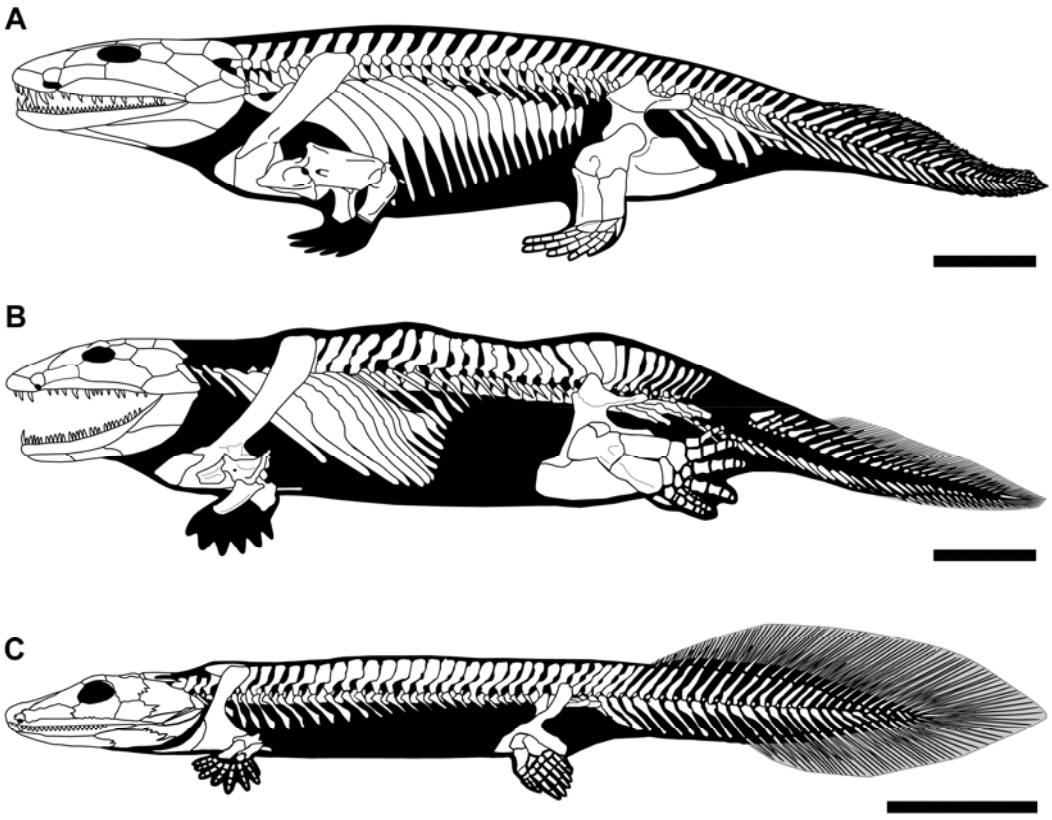



**FIGURE III.3.5.4.1. Tetrapoda**. **A.** *Ichthyostega*, ancient reconstruction as a fully terrestrial "big salamander" (redrawn and modified after JARVIK, 1996), **B**. *Ichthyostega*, new reconstruction based on a detailed study of its dentition, limbs and axial skeleton (redrawn and modified after AHLBERG *et al.*, 2005), **C**. *Acanthostega* (redrawn and modified after AHLBERG *et al.*, 2005). Scale bars equal 10 cm.

Tetrapods originate during the Middle to Late Devonian (but see NIEDZWIEDZKI *et al.*, 2010 for an earlier evidence of their appearance) possibly in Euramerica (CLÉMENT *et al.*, 2004). Considering the morphological convergences observed in other large Devonian tetrapodomorphs, such as rhizodontids, tristichopterids, and "elpistostegalians" it is currently admitted that tetrapods arose out of one of several similar evolutionary 'experiments' as large aquatic tetrapodomorph predators with reduced median fins, among other convergent characters (AHLBERG & JOHANSON, 1998).

The best-known Devonian tetrapods with relatively well-preserved postcranial material are *Ichthyostega* and *Acanthostega* from the Famennian of East Greenland (SÄVE-SÖDERBERGH, 1932; JARVIK, 1952), and *Tulerpeton* from the Famennian of Russia (LEBEDEV & COATES, 1995). *Acanthostega* is considered as the sister group of *Ichthyostega, Tulerpeton* and all post Devonian tetrapods.

The fin-limb pattern of tetrapods is characterized by the presence of digits in the paired limbs. Following COATES *et al.* (2002:394) definition I regard digits as "the combination of two or more spool-shaped bones/cartilages articulating one-to-one proximodistally, occurring as an anteroposteriorly arranged set or series radiating from the distal end of the limb, and bearing no simple ratio of unit-to-unit correspondence with more proximal limb parts". These criteria are more useful to distinguish between digits and endoskeletal radials in the paired fins of derived sarcopterygians when they occur in conjunction with lepidotrichia as in rhizodontids, "osteolepiforms", and "elpistostegalians". Moreover, digits are only present in appendages lacking fin rays and scales, which implies that paired fins of crownward tetrapodomorphs such as "elpistostegalians" or tetrapods can carry either digits or lepidotrichia, but not both at the same time. This condition raises numerous questions concerning the developmental

relationships between the evolution of digits and the reduction and loss of the lepidotrichia from fishes to tetrapods.

The median fins pattern of early tetrapods consist exclusively of a long, continuous, and well developed diphycercal caudal fin carrying lepidotrichia in both dorsal and ventral lobes, as in *Ichthyostega* and *Acanthostega*. As in "elpistostegalians" ,the dorsal lobe extends more anteriorly than the ventral one. Anal and dorsal fins are absent. Lepidotrichia articulate with a series of caudal fin radials (supraneurals for the dorsal lobe and suprahaemals for the ventral one), which in turn articulate with the neural and haemal spines respectively. This 'fish-like' tail is lost in post Devonian tetrapods where the fin fold supported by endoskeletal radials and dermal lepidotrichia is replaced by an epidermal fin fold without osseous dermal components, as that of extant aquatic salamanders (but see CLACK, 2011 for the possible evidence of the presence of supraneural radials in a Carboniferous embolomere).

Early tetrapods present a large array of scale morphotypes. Devonian tetrapods (such as *Ichthyostega*, *Acanthostega*, and *Tulerpeton*) possess rounded, ovoid, or spindle-shaped scales, whereas certain Carboniferous and younger tetrapods show a recovery of a 'squared' morphotype different from the plesiomorphic rhombic morphotype of their fish relatives. Ornamentation is usually absent, the scales being solely composed of bone. Histologically, the scales of tetrapods are extremely simple compared with those of other sarcopterygians; enamel and dentine are absent as well as the basal isopedine layer made of lamellar bone (see Paper III for further details).

**DEFINITION OF TETRAPODA** – There is currently a debate on the proper definition of the taxon Tetrapoda. Three approaches exist: a 'key-character', apomorphy-based definition (i.e., the clade containing all vertebrates that possess, or have possessed, limbs with digits) (e.g., AHLBERG & CLACK, 1998), a 'crown-group', node-based definition (i.e., the last common ancestor of extant amniotes and lissamphibians, and all its descendants) (LAURIN & ANDERSON, 2004), and a 'total-group', branch-based definition (i.e., the clade containing the last common ancestor of the crown group and all taxa that are more closely related to it than to the living sister-group of Tetrapoda, the Dipnoi, and all its descendants) (PATTERSON, 1993).

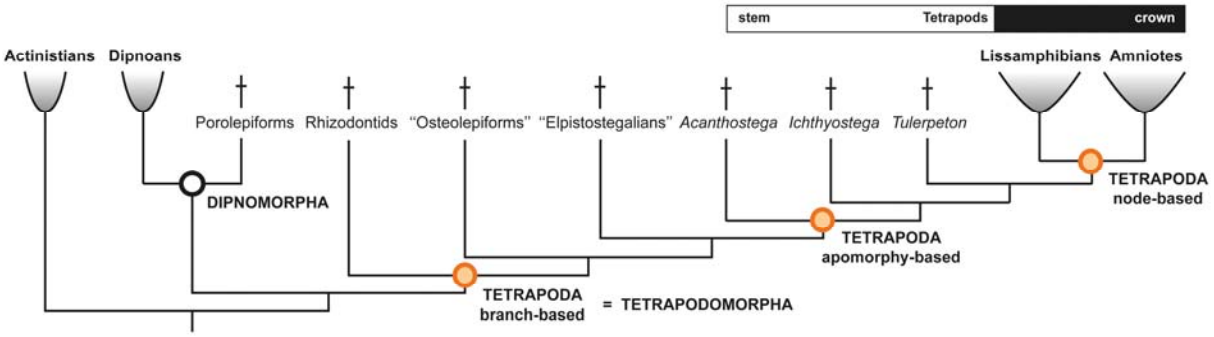



**FIGURE III.3.5.4.2. The three debated definitions of the taxon Tetrapoda** as evidenced in a consensual cladogram of sarcopterygian interrelationships. Note that the branch-based definition corresponds to the Tetrapodomorpha (i.e., all sarcopterygians more related to tetrapods than to dipnoans); the apomorphy-based definition comprise the common ancestor of *Acanthostega* and extant tetrapods and all of their descendants; and the node-based definition considers only crown group tetrapods, excluding Devonian taxa. Crosses denote extinct taxa.

I personally consider the 'crown-group' definition as too reductionist since it excludes Devonian tetrapods such as *Acanthostega*, *Ichthyostega* and *Tulerpeton* (which clearly possess limbs with digits) that are capital for our understanding of the early

evolution of the group. On the other hand, the 'total-group' definition is too inclusive since it comprises many fossil forms that clearly do not have limbs with proper digits such as rhizodontids, "osteolepiforms", and "elpistostegalians". In my opinion, this 'total-group' definition is better assessed by the clade Tetrapodomorpha (AHLBERG, 1991). Therefore I will thereafter consider as tetrapods all terrestrial or aquatic vertebrates possessing limbs with digits and including the last common ancestor of *Acanthostega*, the sister-group of the others tetrapods for which digits have been described, and all its descendants.

Nonetheless, this definition is problematic when we consider incompletely known early 'tetrapods' such as *Obruchevichthys* (VOROBYEVA, 1977a), *Metaxygnathus* (CAMPBELL & BELL, 1977), *Hynerpeton* (DAESCHLER *et al.*, 1994), *Elginerpeton* (AHLBERG, 1995), *Ventastega* (AHLBERG *et al.*, 1994, 2008) or *Densignathus* (DAESCHLER, 2000). These forms are identified as tetrapods relying on their lower jaw morphology (AHLBERG & CLACK, 1998), among other characters from the shoulder girdle and limb endoskeleton (SHUBIN *et al.*, 2004). Valid tetrapod's characters as they may be, they blur the limit between limbed tetrapodomorphs (i.e., tetrapods *sensu* the 'key-character' definition based on the presence of digits) and finned crownward tetrapodomorphs (i.e., "elpistostegalians") that, even showing a highly developed paired fin endoskeleton approaching the tetrapod condition, still retain lepidotrichia on their fins.

Recent discoveries of finned "elpistostegalians" such as *Tiktaalik* show that there is possible that Late Devonian forms would present a mix of primitive and derived character states for tetrapods that can only be identified as being 'fish-like' or 'tetrapod-like' when the entire anatomy of the animal is discovered (e.g., the detailed study of *Elpistostege* changed its phylogenetic position from an early 'amphibian' to a finned "elpistostegalian") (SCHULTZE & ARSENAULT, 1985). *Ergo* a 'tetrapod lower jaw' could well

be associated with a finned animal yet to be discovered and, accordingly, would partially invalidate the attribution of a fossil form to the Tetrapoda based solely on its lower jaw anatomy or any other isolated cranial or postcranial character. Given the current level of knowledge on Devonian tetrapod postcranial remains, neither the 'crown-group' nor the 'total-group' definitions can be applied unambiguously to the early tetrapods. Therefore, only the discovery of relatively complete early tetrapod material, and more particularly of appendicular material, would confirm the unambiguous validity of the 'key-character' definition of Tetrapoda.

## IV. THE 'FISH-TETRAPOD TRANSITION'

The evolutionary transition from fishes to land vertebrates has been one the major scientific and philosophical issues in the history of mankind. From the Ancient Greece philosophers such as ANAXIMANDER OF MILETUS (610-546 BC), who first proposed the descent of men from aquatic fish-like animals, to today's ground-breaking research in developmental genetics, which is beginning to unravel certain aspect of the genetic basis for morphological change, the origin of tetrapods will continue to puzzle scientists for many years to come (JANVIER, 2010).

Since the first fossil findings of early tetrapods, many hypotheses have been proposed to explain why vertebrates grew legs and moved onto land. For sure, every vertebrate palaeontologist has his own theory, but these are the hypothesis explaining the origin of tetrapods most commonly found in recent literature (completed after CLACK, 2002a):

- To get back into the water under arid conditions (ROMER, 1945)
- "Limbs" initially for burrowing in the mud (ORTON, 1954)
- Competition and/or predation with other aquatic forms (MCNAMARA & SELDEN, 1993)
- To escape oxygen-depleted water
- Feeding on terrestrial or semi-terrestrial food sources (MARKEY & MARSHALL, 2007)
- Increase in body temperature (increase in digestion rate, speed development, etc.) (CLACK, 2002a; CARROLL *et al.*, 2005)
- Spawning or escaping from predators on land
- Grip to the bottom or to aquatic vegetation against currents (STEYER, 2012)
- Stability in water (limbs as ballasts) (STEYER, 2012)
- Amplexus in the water (STEYER, 2012)

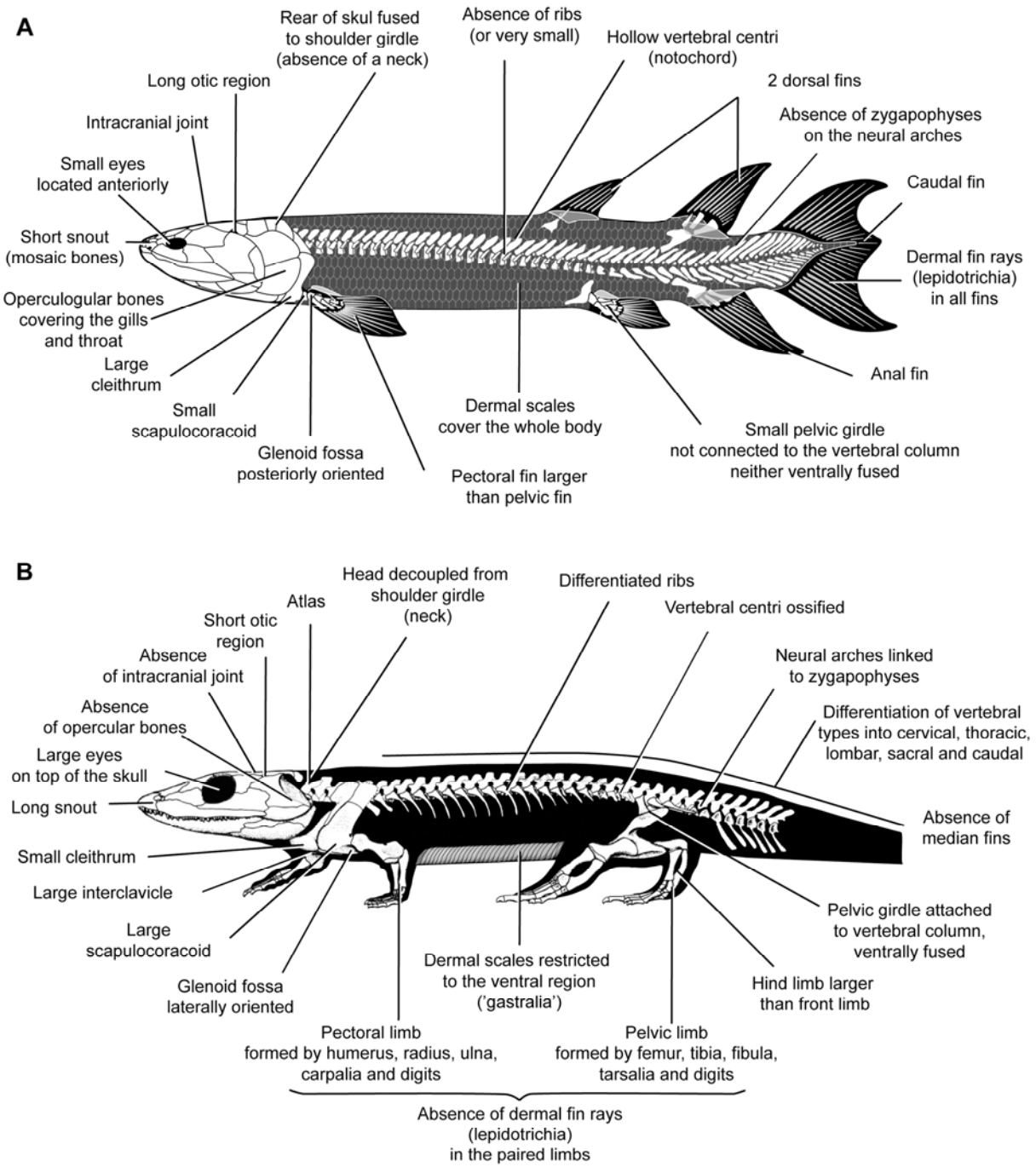



**FIGURE IV.1. The 'fish-tetrapod transition'**. Diagram illustrating the main anatomical differences between a 'fish' and a 'tetrapod'. **A**. An archetypical sarcopterygian fish (*Eusthenopteron*), **B**. An archetypical tetrapod (*Dendrerpeton*). Redrawn and modified after HOLMES *et al.,* 1998; CLACK, 2002a; BENTON, 2008.

Our knowledge on early tetrapods, especially Devonian ones, has dramatically increased since the nineties with the redescription of the two most completely known Devonian tetrapods *Acanthostega* and *Ichthyostega* (CLACK, 1988; COATES & CLACK, 1990; JARVIK, 1996; COATES, 1996; CLACK, 2002b, 2003; AHLBERG *et al.*, 2005). Today early tetrapod research goes through a renaissance by the combined increase of general interest, methodologies, and available fossil material. We currently know fourteen Devonian tetrapod genera, distributed worldwide (BLIECK *et al.*, 2010; CLACK *et al.*, 2012). However, several questions remain to be answered concerning key aspects of their anatomy, physiology, and way of life. The study of scale and fin ray morphology and evolution will surely add new and relevant data in order to better understand the 'fish-tetrapod transition' (Fig. IV.1).

## IV.1. LIFE ON LAND

At first glance, it is difficult to imagine more different habitats than water and land, and yet vertebrates managed not only to pass from one to the other, but also to settle on land, and even to secondarily return to water in multiple occasions (MAZIN & BUFFRENIL, 2001). Almost every aspect of animal biology changed during the 'terrestrialization' process (i.e., the transition between water and another fluid: air) (JANVIER, 2010). For instance, new modes of locomotion evolved as well as new ways of breathing, feeding, sensing prey and predators, water balance control, and reproduction. When all these problems of life on land are considered, it may seem surprising that vertebrates ever left the water (and yet here we are).

Devonian tetrapods are generally considered as mainly aquatic animals (AHLBERG & MILNER, 1994), as evidenced by the retention of a series of primitive traits such as a

caudal fin supported by lepidotrichia, a lateral line system, and internal gills in *Ichthyostega* and *Acanthostega* (COATES & CLACK, 1991; COATES, 1996; CLACK *et al.*, 2003). The well-developed caudal fin suggest that *Ichthyostega*, but more particularly *Acanthostega* could have swum by powerful sweeps of their tails, as modern crocodiles. In addition, the orientation of the shoulder and pelvic girdles, and the size and shapes of the limb bones, show that the limbs of Devonian tetrapods were more suited to swimming that to walking. Limbs were certainly used in turning and controlling of the pitch, yaw, and depth of the animal in the water column.

The polydactylous hand and foot (8 digits in *Acanthostega*, 7 in *Ichthyostega,* and 6 in *Tulerpeton*) (COATES & CLACK, 1990; JARVIK, 1996; LEBEDEV & COATES, 1995, respectively) were broad and flat, and used more as paddles in the water than weight bearing structures on land. Nevertheless, it is possible that these animals could have been able to venture onto land in certain sporadic occasions. In the case of *Ichthyostega* it has been proposed that differentiated presacral vertebral column would have allowed vertical flexion of the lumbar region in an 'inchworm' movement, as in modern seals (AHLBERG *et al.*, 2005). On the other hand, *Acanthostega* would have certainly been unable to leave the water, although it could have 'walked' on the bottom of streams with the caudal fin floating as revealed by Devonian trackways (CLACK, 1997; NIEDZWIEDZKI *et al.*, 2010).

However, there are certain problems related with land incursion or long-time establishment on land, and these deal with the primitive fish-like traits of early tetrapods. In the water, weight is minimized by the ARCHIMEDES principle of buoyancy, whereas on land the body is pulled downwards by gravity. Major changes are needed in the limbs, vertebral column, muscles, and other internal organs to cope with these new forces. However, Devonian tetrapods still retain a fish-like body appearance despite the

acquisition of limbs with digits, among other features. The dermal scales and the fin rays belong to these fish-like traits that would have certainly slowed tetrapods during their incursions on land. Indeed, a dragging, fin ray-supported caudal fin is a continuous source of injuries on land, and fish-scales as present in their tetrapodomorph relatives are not suitable to prevent the body walls and the belly from compression outside the water (with the possible exception of the thick rhombic scales of "elpistostegalians", *pers. obs*.). Fin rays and scales evolved, and were eventually loss, during the 'terrestrilization' of tetrapods to cope with the problems related to life on land (Papers III and IV).

## IV.2. FINS INTO LIMBS

Leaving aside the 'problematic' primitive fish-like features of Devonian tetrapods, here I shall focus in one (if not the most) important aspect of the 'fish-tetrapod transition' that combines both paleontological and developmental genetic evidences: the evolutionary transformation from fish fins into tetrapod limbs. I will present the main issues associated with the application of developmental studies to palaeontological evidences of character evolution in relation to the origin of tetrapods.

### IV.2.1. PALEONTOLOGICAL EVIDENCES

When examining the structure and arrangement of bones in the appendicular skeleton of tetrapodomorphs it becomes apparent that the same bones can be recognized in the limb of a tetrapod and the fin of a tetrapodomorph fish. A single heavy bone (the stylopod, humerus or femur) connects with the body through a girdle

(pectoral or pelvic) by a monobasal articulation, next there are two lighter bones (the zeugopod, radius and ulna or tibia and fibula) that combine support with manoeuvrability, and finally, in tetrapods, the most distal bones form the wrist (carpals or tarsals) and the digits (the autopod).

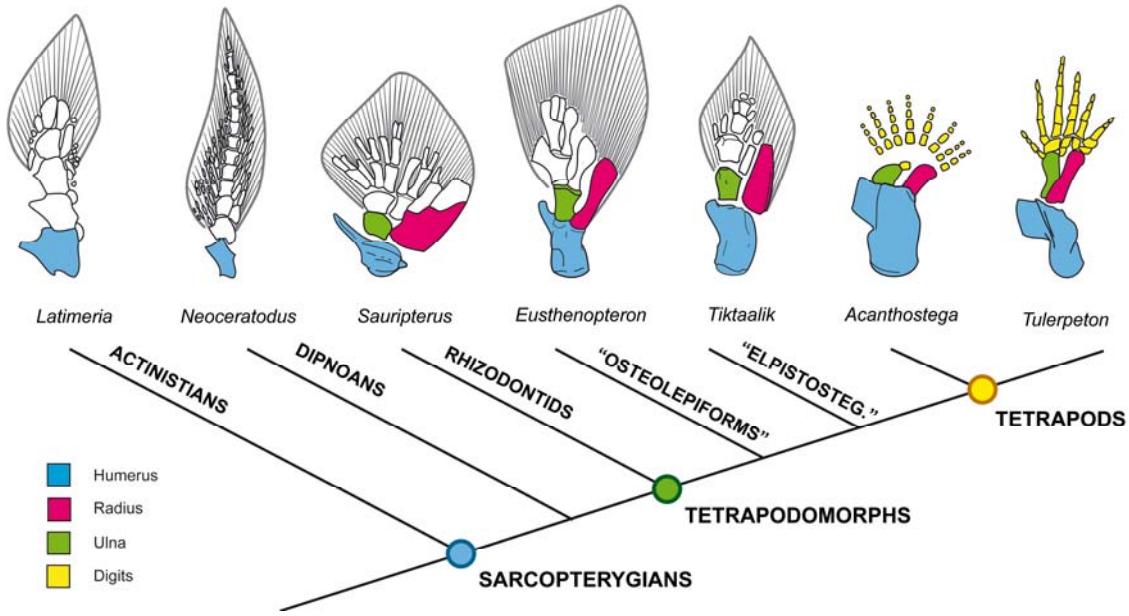



**FIGURE IV.2.1.1. The evolution of paired fins in sarcopterygians** illustrating the arrangement of the endo and dermoskeleton in the fore fin/limb. Taxa are plotted on a consensual phylogeny of sarcopterygian interrelationships. Redrawn after JARVIK, 1980; COATES, 1996; LEBEDEV & COATES, 1995; COATES *et al.,* 2002; DAVIS *et al.,* 2004; SHUBIN *et al.,* 2006.

Although the homology of proximal bones in tetrapod limbs and tetrapodomorph paired fins has become well established (COATES *et al.*, 2008), much debate persists on the homology between fin distal radials and digits. Indeed, digits do not correspond, either in position or in formation, with the radials resulting from the 'normal' branching pattern of sarcopterygian fins. Most palaeontologists have thus regarded digits as evolutionary novelties (BOWLER, 2007). However, this does not imply that the genetic

mechanisms underlying digit formation could not have been co-opted and slightly modified from those patterning the bones of distal portion of the tetrapodomorph fins (SHUBIN *et al.*, 2006; FRIEDMAN *et al.*, 2007).

Tetrapodomorph paired fins/limbs show a proximal stability and a distal instability, i.e., distal structures can be more easily modified and lost than proximal ones (WAGNER & LARSSON, 2007). For instance, the evolution of the number of digits is a well-known tetrapod feature. Devonian tetrapods show polydactylous limbs (COATES & CLACK, 1990; LEBEDEV & COATES, 1995) whereas reduction in digit number and establishment of pendactyly occurred after the Devonian and probably evolved independently in reptile and lissamphibian lineages (COATES, 2004).

This distal instability can also be applied to the dermal fin web since it corresponds to the distal-most structure of a fin and its loss in tetrapods did not seem to affect the most-proximal elements (stylopod and zeugopod). The distal endoskeleton, on the contrary, was significantly modified with the appearance of digits (autopod) (LARSSON, 2007) and it has been proposed that the lack of dermal fin rays could have somewhat enhanced the proliferation of the endoskeleton (THOROGOOD, 1991; SORDINO & DUBOULE, 1996). However, fossil evidences show that modifications of the distal endoskeleton are not directly dependent on the absence of a fin web, as seen in the extensively ossified 'paddles' of rhizodontids like *Sauripterus* (DAVIS *et al.*, 2004) and the mobile distal elements of the 'flimbs' of "elpistostegalians" like *Tiktaalik* (SHUBIN *et al.*, 2006).

One thing is nonetheless clear; the fossil record has not yet provided a form of tetrapodomorph fish with both digits and fin rays at the same time, thus suggesting that although the expansion of the distal endoskeleton is compatible with a dermal fin web, the formation of digits is not. Moreover, fin ray reduction is known in the paired fins of

the extant dipnoans *Lepidosiren* and *Protopterus* (COATES & RUTA, 2007) and in certain extant actinopterygian clupeiforms (e.g., *Sundasalanx*, the dwarf noodlefish). This condition evidences that absence of dermal fin rays can occur without any resemblance of digit evolution.

The fossil record also shows that loss of the dermal lepidotrichia occurs simultaneously in pectoral and pelvic fins (COATES *et al.*, 2002) thus suggesting that pectoral and pelvic fins are serial homologs (COATES, 2003). It has also been revealed that the evolutionary 'domination' of pectoral appendages against the pelvic was switched in tetrapods (COATES *et al.*, 2002; BININDA-EMONDS *et al.*, 2008). In tetrapods crownward of *Acanthostega*, morphology and development of the hindlimb seems to overtake that of the forelimb. This led COATES (1994) to suggest that pelvic lepidotrichia may have been lost before pectoral ones. However, there is no way to prove this statement given the current available material of Devonian tetrapods. On the other hand, what has become evident by the discovery of well-preserved early tetrapods is that the maintenance of lepidotrichia in the fish-like caudal fin of *Acanthostega* and *Ichthyostega* strongly suggests that the loss of rays in paired and median fins was independent, probably reflecting a separate genetic control of the paired and tail fins.

Finally the fossil record illustrates the great variability of patterns and distribution of fin elements in tetrapodomorph fishes. When considering forms such as rhizodontids, large tristichopterids, and "elpistostegalians" we see that Late Devonian freshwater ecosystems were the source of major novelties in skeletal and appendage evolution (AHLBERG & JOHANSON, 1998; SHUBIN, 2002). Indeed in Palaeozoic tetrapodomorphs dwelling in shallow waters the unit that interacts with the substrate is a combined element consisting of contributions from both the dermo- and endoskeleton. In these forms the paired appendages are a higher order unit composed of two types of

skeletal tissues in which the function of the fin bones in locomotion is mediated by the dermal fin rays. In tetrapods, this is not the case since the loss of the fin web implies that the endoskeleton interacted more directly with the substrate, enabling a whole new set of morphofunctional applications for limbs. In order to fully reconstruct the ecological scenario of the 'fish-tetrapod transition', further studies should focus on the function of the closely associated endoskeletal bones and fin web in Devonian tetrapodomorphs. Moreover, the morphological patterns present in recently discovered tetrapodomorph fishes (e.g., *Sauripterus, Gogonasus, Tiktaalik*) need also to be taken into account by developmental biologists if we are to study the genetic basis and evolution of these morphologies and the origin of the tetrapod limb.

### IV.2.2. GENETIC EVIDENCES

The tetrapod limb bud is probably the developing structure for which more molecular data are available in terms of understanding patterning mechanisms in vertebrate embryos (e.g., SHUBIN *et al*., 1999; ZÁKÁNY & DUBOULE, 2007). In the last two decades, the study of limb development has benefited from a new synthesis of developmental and evolutionary biology based on the reinterpretation of the fossil record and on new discoveries from developmental genetics (e.g., GILBERT, 2003a; YANO & TAMURA, 2012). The analysis of the fossil record (especially of Late Devonian tetrapods discovered in recent years) has helped to establish the evolutionary history of the fins into limbs transition, and developmental biologists have attempted to explain it in terms of changes in the activity of genes involved in embryonic development (CAPDEVILLA & IZPISÚA-BELMONTE, 2000, 2001).

As previously stated, tetrapod limbs show a proximal stability and a distal instability. Indeed, many of the developmental studies on the evolution of the tetrapod limb have focused in the distal portion of the limb (such as surnumerary digits or their loss) (LITINGTUNG *et al.*, 2002). Similarly, the differences between tetrapod limbs with digits and fish fins with rays also lie in the distal-most portion of the appendage. These changes deal with, among other features, the fate of the ectodermal apical ridge (AER) and the establishment of the apical fold (AF) in fishes, HoxA-D genes expression patterns along the proximo-distal and antero-posterior axes, and Shh expression in the zone of polarizing activity (ZAP) (e.g., FROMENTAL-RAMAIN *et al.*, 1996; MARTIN, 1998; DUDLEY *et al.*, 2002; HINCHLIFFE, 2002; DAHN *et al.*, 2007; DAVIS *et al.*, 2007; AHN & HO, 2008).

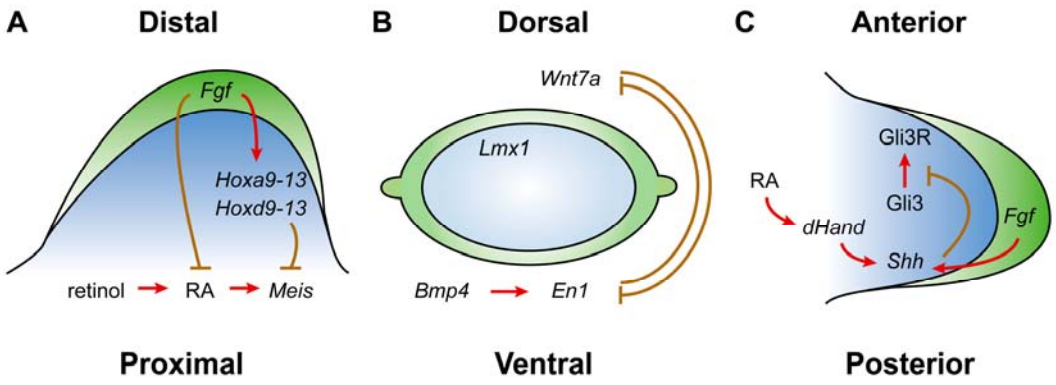



**FIGURE IV.2.2.1. Key genes in fin/limb buds implicated in axis patterning. A.** Signaling cascades for limb outgrowth and specification of position along the proximo-distal axis. **B.** Signaling cascades for limb specification along the dorso-ventral axis. **C.** Signaling cascades for establishment of antero-posterior pattern of limb bud. The AER is represented in green, the underlying mesenchyme of the limb bud is in blue. Redrawn and modified after TANAKA & TICKLE, 2007.

The limb bud is a structure patterned along three axes: proximo-distal, antero-posterior, and dorso-ventral. Much of the recent work of developmental biology has focused on the identification of the genetic pathways involved in the patterning and

outgrowth along each of these axes (Fig. IV.2.2.1). It has also been assumed that molecular changes in these pathways would have morphological consequences, at first interpreted in terms of malformations, but recently considered under an evolutionary perspective. Certain 'teratological' morphologies have been mirrored with fossil morphologies (Fig. IV.2.2.2). The study of key molecules determining the polarity, patterning, and outgrowth of the fin bud could be informative of the microevolutionary genetic changes leading to macroevolutionary morphological consequences.

However, the search for morphological similarities between atavic laboratory animals and fossil taxa has highlighted a problem in the use of developmental biology to explain morphological diversity (Fig. IV.2.2.2). The problem is: we have absolutely no clue whether the mutant genes or pathways responsible for these odd conditions are in fact the underlying cause for the morphologies seen in the fossil record. Therefore every categorical explanation about the evolution of a certain structure (e.g., the loss of fin rays in tetrapods) by a *single* genetic factor might be taken with caution. Moreover, it is also known that certain of these pathways are redundant and therefore affecting a certain molecule could not have the expected morphological result because its effect might be attenuate by a different molecule with similar action. This is especially true in structures that are vital for the survival of the organism since the earliest stages of development (e.g., the caudal fin is among the first structures to develop in larval zebrafish and its crucial function in swimming is well known) (KIMMEL *et al.*, 1995).

In conclusion, organic development is a highly complex process of which we are but beginning to understand the main aspects. If we are to study the implications of developmental changes on evolutionary modifications we shall narrow our expectations and try not to categorize molecules, but developmental pathways through molecular coordination and cell-to-cell interactions.

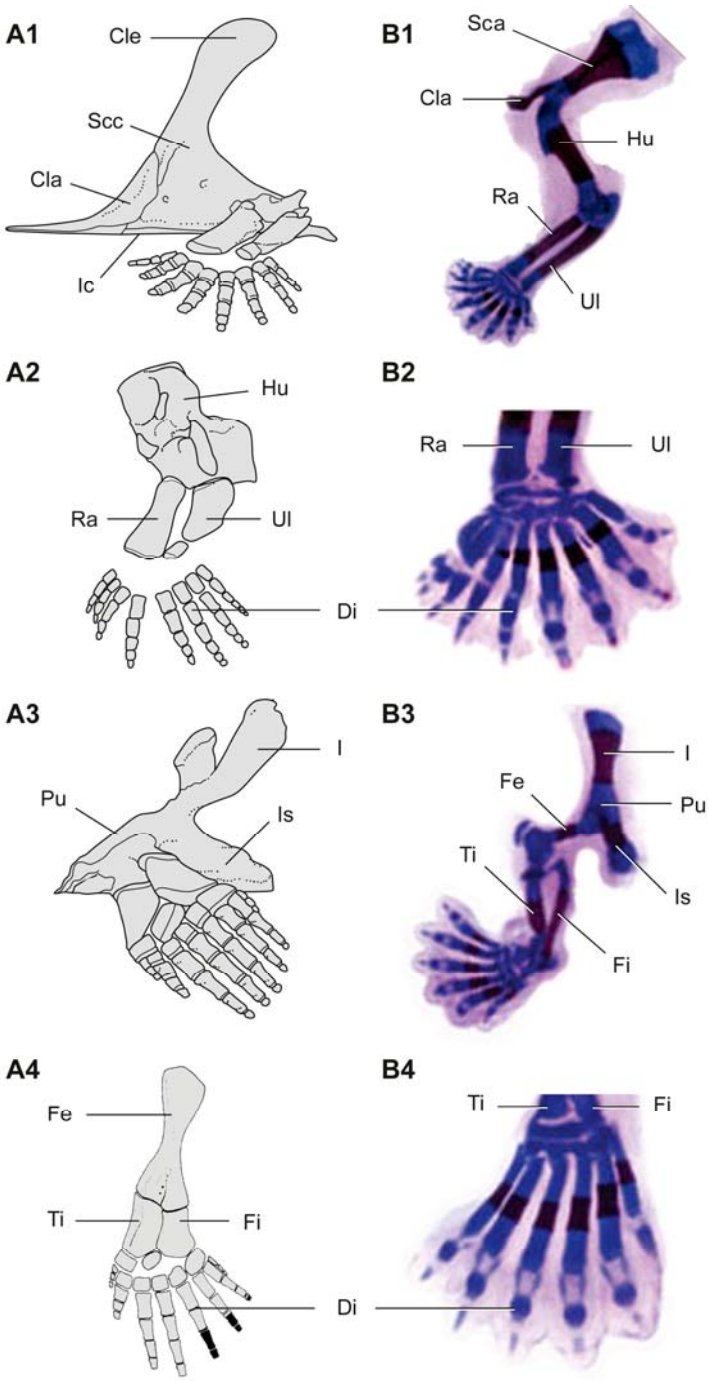



**FIGURE IV.2.2.2. Is *Acanthostega* a Shh$^{-/-}$ Gli3$^{-/-}$ mouse?** Comparison between **A.** Fossil morphologies (e.g., the Devonian tetrapod *Acanthostega*) and **B.** Atavic morphologies resulting in genetic knockdown manipulations (e.g., Shh and Gli3 mutations) in the mouse, *Mus musculus*. **1.** Pectoral (shoulder) girdle and forelimb, **2.** Forelimb, **3.** Pelvic girdle and hindlimb, **4.** Hindlimb. **Abbreviations: Cla**, clavicule; **Cle**, cleithrum; **Di**, digits; **Fe**, femur; **Fi**, fibula; **Hu**, humerus; **I**, ilion; **Ic**, interclavicle; **Is**, ischium; **Ti**, tibia; **Pu**, pubis; **Ra**, radius; **Ul**, ulna; **Sca**, scapula; **Scc**, scapulocoracoid. Modified after COATES, 1996; LITINGTUNG *et al.*, 2002.

# V. THE DERMOSKELETON

The dermoskeleton has always figured prominently in studies of the evolution of fishes because it is the part of the organism most often preserved in the fossil record (e.g., GOODRICH, 1904, 1907). Since the nineteenth century, morphological differences in dermal ossifications (such as scales and fin rays) and histological variations of their microstructure have been used in fish classifications of high taxonomical rank (AGASSIZ, 1833-44); the importance of the dermoskeleton in systematic reconstructions is still greatly recognised today (e.g., DONOGHUE *et al.*, 2006; FRIEDMAN & BRAZEAU, 2010).

Here I will present a general survey of the dermoskeleton and furnish the definitions of the main terms used in the description of skeletal tissues followed in the Papers composing this thesis. I shall limit to the anatomical, histological and cytological levels of observation, which are the only ones that are preserved in fossils (FRANCILLON-VIEILLOT *et al.*, 1990). Finally I will detail the structure, function, development, and evolution of the two dermoskeletal components of interest in this dissertation: the scales and the fin rays.

## V.1. DERMOSKELETON VS. ENDOSKELETON

The skeleton of vertebrates is divided in two systems: the endoskeleton (internally) and the dermoskeleton (externally). The term endoskeleton refers to the portion of the skeleton that is deeply embedded in the body. Its antonym, the 'exoskeleton', has been generally applied in vertebrates to the more external skeletal components, such as dermal bones, scales and teeth. However, the term 'exoskeleton' has often been synonymized with the dermoskeleton. This synonymy is misleading and

should be avoided (PATTERSON, 1977). Indeed, 'exoskeleton' should be restricted to hard tissues that differentiate exterior to the epidermis (such as hard, non-mineralized keratinous derivatives like horns, claws, and nails). Dermoskeleton would thus include the superficial mineralized components of the vertebrate skeleton that differentiate within, or close to, the dermis (such as dermal bones, teeth, scales, and fin rays).

The dermoskeleton was the first part of the vertebrate skeleton to appear in a mineralized form (Fig. V.1.1). First unequivocal record of a dermoskeleton is the dermal armour of Palaeozoic "ostracoderms" that show different arrangements of enamel, dentine, and bone in their scales and head shields (JANVIER, 1996). The endoskeleton evolved afterwards as a way of strengthening the body from within. In gnathostomes, the dermoskeleton has gradually diminished its importance relative to an extensively developed endoskeleton (JARVIK, 1980; JANVIER, 1996).

The capacity of ossification is unique to vertebrates. Ossification of both dermal and endoskeletal elements is a living and controlled process defined as "the calcification of specific organic matrices made of collagen, non-collagenous proteins and complex glucides, by mineral deposits consisting primarily of poorly crystalline hydroxyapatite, a calcium phosphate" (FRANCILLON-VIEILLOT *et al.*, 1990: 473).

Four classes of mineralized components are found in vertebrates: *bone*, *cartilage*, *dentine*, and *enamel* (HALL & WITTEN, 2005). Cartilage and bone are usually considered as skeleton-forming products (skeletogenic) whereas enamel and dentine are both skeleton and tooth-forming products (odontogenic). Enamel and dentine arose evolutionarily together with bone in the dermal skeleton of early vertebrates (DONOGHUE *et al.*, 2002) (Fig. V.1.1). Cartilage, on the other hand, provided the basis for the second vertebrate skeletal system, the endoskeleton (SMITH & HALL, 1990), and hence does not belong to the dermoskeleton.

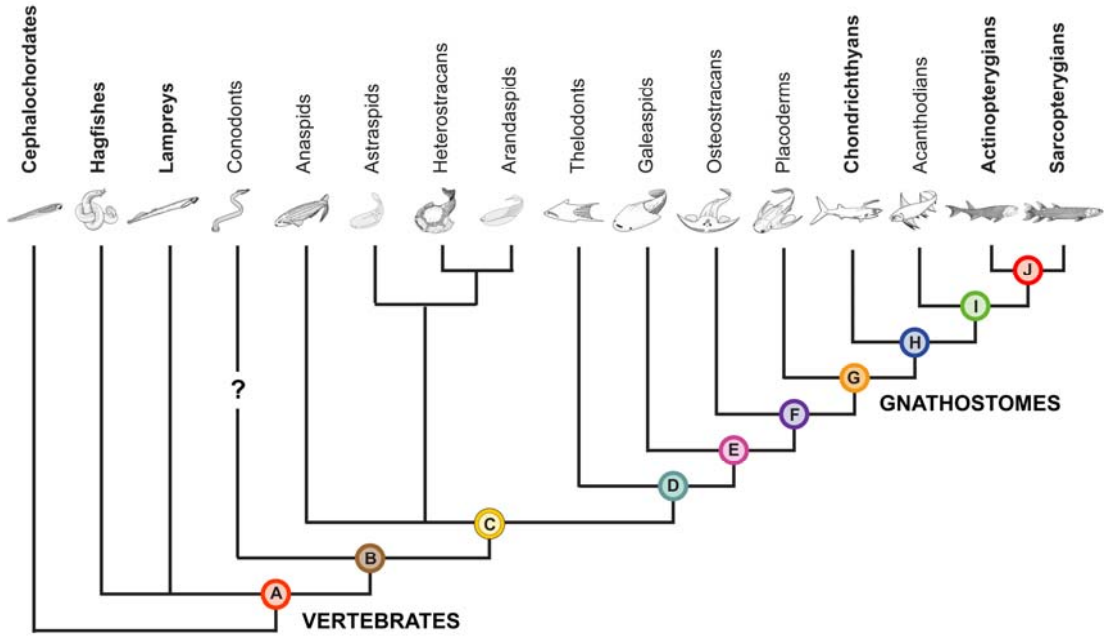



**FIGURE V.1.1. The evolution of the dermal skeleton** evidenced in a consensual cladogram of the main groups of vertebrates. Lettered nodes refer to significant events in the skeletal system of vertebrates. Extant taxa in bold. **A.** Origin of the vertebrate skeleton including a notochordal sheath, fibrous fin rays, neurocranium and splanchnocranium though entirely composed of unmineralized cartilage, origin of neural elements in the axial skeleton (in lampreys). **B.** Origin of a mineralized skeleton composed of dentine and enamel comprising the 'odontode developmental module' first manifested in the splanchnocranium (although the presence of "dentine" and "enamel" in conodonts as been regarded as non homologous with those of vertebrates, TURNER *et al.*, 2010). **C.** Origin of a mineralized dermoskeleton composed of odontodes (dentine and enamel) supported by extensively developed dermal bone. **D.** Odontodes associated with the splanchnocranium, including either the gill arches or the nasohypophyseal openings. **E.** Origin of perichondral bone, mineralized endoskeleton, neurocranium composed of globular calcified cartilage. **F.** Origin of an appendicular endoskeleton (with equivalents of the scapula and coracoid), properly mineralized neurocranium and splanchnocranium, cellular dermal bone in the dermo and endoskeleton. **G.** Origin of a mineralized axial skeleton, appendicular skeleton and fin radials, ventral vertebral elements, centra (arcocentra), and "teeth". **H.** Dental elements (teeth) associated with the splanchnocranium including branchial arches. **I.** Neurocranium composed of distinct ossifications, splanchnocranium well ossified. **J.** Origin of endochondral bone, dermoskeleton and endoskeleton well ossified. Redrawn and modified after DONOGHUE & SAMSON, 2002; DONOGHUE *et al.,* 2006.

Dermal bones are commonly (but not always) flat and they lack mobile joints. They form in the dermis (the deepest portion of the skin) via direct membranous ossification, without previous differentiation into transitory cartilage. Dermal bones may become secondarily associated with endoskeletal elements, fusing with them to form composite or mixed bones (e.g., the 'angular' bone of the teleost actinopterygians). Commonly, dermal bones are superficially ornamented (e.g., tubercles, ridges, pits, grooves, etc.) either by odontogenic components associated with the bone (e.g., ganoine, cosmine, dentine tubercles and/or ridges in the scale of fishes) or by exposed rugosities and superficial folds of the bone itself (e.g., bony ridges and grooves in the dermal skull bones of tetrapods).

The contribution of odontogenic components (i.e. enamel and dentine) to the dermal bones is commonly present in fishes, especially in their scales. The dentary components may be organized as superficial isolated simple dentary units (odontodes), or they may fuse together, following different patterns in various lineages, to form 'odontocomplexes' (*sensu* ØRVIG, 1968). In tetrapods, the odontogenic components of the dermal skeleton are lost except for those located around the mouth cavity (i.e., teeth).

### V.2. HISTOLOGICAL LAYERS

As previously stated, the dermoskeleton shows three of the four classes of mineralized components in vertebrates: *bone*, *dentine*, and *enamel*. Their variable arrangement, distribution, and combinations between them define the different histological layers encounter in every description of osseous dermal products, and most notably, in the paleohistological studies on the scales and fin rays.

Here I will introduce the main terms dealing with histological descriptions used in this thesis. I will divide them into dermal products, for which I shall describe the very nature of each mineralized tissue of the dermoskeleton, and topological terms, which comprise combinations of tissues (e.g., cosmine) or bony layers that receive particular names depending on their location (e.g., isopedine).

### V.2.1. DERMAL PRODUCTS

**BONE** – Bone is a vascularized, supporting skeletal tissue consisting of cells and a mineralized extracellular matrix. Bone is deposited by bone-forming cells (*osteoblasts*), which, when they cease dividing, are embedded in the bone matrix and become *osteocytes* that reside in an osteocytic lacuna. The thin cytoplasmic processes of the *osteocytes*, the *canaliculi*, permeate the matrix and participate in bone nutrition.

The first bone matrix deposited is unmineralized and is known as *osteoid*. Subsequently, *osteoid* is impregnated with hydroxyapatite and mineralizes to form the bone. Eventually, bone is modelled, remodelled, and/or removed by *osteoclasts* (and sometimes by *osteocytes*). Bone grows by peripheral accretion due to the activity of a *periost* that overlays the bone (FRANCILLON-VIEILLOT *et al.*, 1990; RICQLÈS *et al.*, 1991).

Three modes of arrangement have been defined for the collagenous fibres in the bony matrix (MEUNIER, 2011):

- **Woven-fibered bone:** collagen fibres form an unordered intermingled network;
- **Pseudo-lamellar bone:** collagen fibres are arranged with the same orientation in successive strata and are parallel to each other;
- **Lamellar bone:** collagen fibres are arranged in strata whose orientation differs between two successive strata with an angle of about $90^0$.

Bone is as an aerobic tissue with high oxygen consumption. It is not only a support structure but it also plays a major role in metabolic regulation of mineral homeostasis as a storehouse for calcium and phosphorous. Bone remodelling is under hormonal control and is dependent on environmental pressures, such as ion deprivation.

**DENTINE** – Dentine is a tubular mineralized tissue characteristic of teeth and also present in the scales of early fishes. Dentine is a primary tissue of the vertebrate dermal skeleton, and thus is both an odontogenic and a skeletogenic tissue. Dentine is produced by *odontoblasts* but, unlike bone where *osteoblasts* normally become embedded in the matrix, *odontoblasts* remain outside the mineralized matrix, which is, however, penetrated by odontoblast cell processes (i.e., dentine tubules). As are bone and enamel, dentine is produced in two sequential phases; synthesis and deposition of an organic matrix known as predentine is followed by its mineralization by hydroxyapatite to form definitive dentine. Various types of dentine are recognized, mainly depending on the shape and patterns of the odontoblasts process within the matrix (e.g., orthodentine, osteodentine, etc.) (ØRVIG, 1968; SMITH & HALL, 1990; SIRE *et al.*, 2009).

**ENAMEL** – Enamel is a highly mineralized, hard, prismatic, avascular dermal product found in the outer layer of the teeth, scales, and fin rays of vertebrates. Like dentine, enamel is both odontogenic and skeletogenic. Enamel is unique in being the only non-collagenous mineralized vertebrate skeletal component; cells are also lacking. Because of its very high mineral content, enamel is much more resistant to wear than dentine. In contrast to the other three mineralized tissues, enamel is an epithelial component produced by *ameloblasts*. Enamel formation (amelogenesis) consists of two phases:

deposition of an organic matrix and subsequent mineralization of the matrix during which organic matrix is completely removed to facilitate the precipitation of the inorganic substance.

***Enameloid*** is a puzzling enamel-like mixed product of epithelial-mesenchymal origin that resembles enamel both topologically and functionally. Enameloid is deposited the combined action of *ameloblasts* and *odontoblasts* and shows cellular processes from the underlying dentine. In living vertebrates, enameloid is present in chondrichthyans, actinopterygians and larval stages of caudate amphibians. SMITH *et al.* (1972) identified enameloid in the scales of *Latimeria*, although CASTANET *et al.* (1975) consider it enamel. Enamel and enameloid are surely homologous tissues, but their origin is still unclear.

### V.2.2. TOPOLOGICAL TERMS

Dermal ossifications (e.g., scales) can be usually divided into two portions in transversal section: superficial and basal. Each portion follows its own developmental patterns and both become fused during development. Since each portion is somewhat independent in its formation, subtle heterochronic changes can lead to morphological differences in one portion without necessarily affecting the other. Each portion is in turn composed of different dermal tissues with particular arrangement and morphologies, whose development is depending on morphofunctional constraints.

The following definitions deal more with scales than with rays. However, the fin rays of Devonian sarcopterygians can also show certain of these tissues (e.g., cosmine). Their presence (or absence) can thus be informative of the developmental relationships between tissues and relationships of homology between scales and fin rays.

#### V.2.2.1. SUPERFICIAL PORTION

**COSMINE** – Cosmine is not a tissue, but an association of tissues. It consists of an external layer of enamel (or enameloid) overlying a layer of dentine that contains a characteristic and complex pore-canal network. The vertical canals of the dentine form flask-shaped chambers that open to the surface through pores in the enamel. The whole system is closely connected to an underlying parallel-fibered (pseudo-lamellar) dermal bone that is richly vascularized through vascular canals contacting the horizontal canals of the dentine (GROSS, 1956; ØRVIG, 1969a; THOMSON, 1975). Cosmine is primitively widespread in fossil sarcopterygians, but has no living homolog among extant osteichthyans. Cosmine characterizes cosmoid scales (*sensu* FRANCILLON-VIEILLOT *et al.*, 1990), yet its function is not clearly known (see Discussion). Cosmine develops only in the exposed area of the dermal bones, scales and fin rays of sarcopterygians, i.e., in the interface between dermis and epidermis.

**SPONGIOSA** – The spongiosa is here considered as the topological term attributed to the middle vascular bone layer of the scales in osteichthyans. The spongiosa is a highly vascularized pseudo-lamellar bone, pierced by numerous primary and secondary osteons, and appearing thus as cancellous in certain taxa. When cosmine is present, the spongiosa is located immediately under the cosmine, the vascular canals of the spongiosa merging with the horizontal canals of the cosmine. However, in the absence of cosmine, the exposed zones of the spongiosa are denser and less vascularized than the deeper parts. Bony tubercles and ridges ornamenting the scales in certain sarcopterygians are also considered to belong to the spongiosa as a sculptured external surface (THOMSON, 1975).

#### V.2.2.2. BASAL PORTION

**ISOPEDINE –** The isopedine is a layer of lamellar bone with a plywood-like arrangement of the collagen plies found in the basal portion of the scales of osteichthyans. The collagen plies can show two kinds of orientation: orthogonal (as in the "osteolepiform" *Osteolepis*) or twisted (as in the extant coelacanth *Latimeria*) (GROSS, 1956; MEUNIER, 1984). Vascular canals can be found in the isopedine, although few in number; certain can open to the exterior through pores in the internal surface of the scales. The isopedine forms the internal surface of the scale. Its thickness and mineralization state can be variable (e.g., in fossil sarcopterygians isopedine is heavily mineralized, whereas in extant sarcopterygians like *Latimeria* and *Neoceratodus*, the isopedine is very lightly or not mineralized at all) (*pers. obs.*). The isopedine is particularly thin at the anterior margin of the scales enabling to see the overlying spongiosa by transparency in certain fossil sarcopterygian scales (JARVIK, 1948; GREINER, 1977).

***Elasmodine*** was first coined by BERTIN (1944) to describe the unmineralized basal layer of lamellar bone of the elasmoid scales of actinopterygians. Although clearly homologous to isopedine in structure and location, SCHULTZE (1996b: 87) proposed a series of differences between the two, pointing to their different origin and tempo of formation. Based on scale development in *Polypterus*, SIRE *et al.* (2009) proposed that elasmodine is a derived form of dentine, that would be located between the spongiosa and the dentine in the primitive osteichthyan scale, and that its similarity with isopedine is convergent in actinopterygians. It is not in the scope of this thesis to settle whether elasmodine is a real dentine-derived tissue or simply a partially unmineralized isopedine. However, key comparative data will certainly be provided by histological studies on stem sarcopterygians that are currently undertaken (QU, *pers. comm.*, 2012).

**BASAL BONE TISSUE** – A woven-fibered bony tissue, receiving numerous Sharpey's fibres usually occupies the lower-most part of the basal portion of the osteichthyan scales. This bony accretion forms the ornamentation of the internal surface of the scales in actinopterygians and sarcopterygians (i.e., the articular ridge of the rhombic scales or the boss of certain rounded sarcopterygian scales). Although its morphofunctional importance is clear in the articulation between scales and in the anchoring point of Sharpey's fibres, its developmental origin is unclear. Histological observations show that it is tightly associated with the isopedine, but also that it can be lost independently of the latter (e.g., in onychodontids, actinistians, holoptychiids, and derived dipnoans).

## V.3. THE SCALES

### V.3.1. FUNCTION

The term 'scale' is confusing; it refers both to the superficial 'scales' of birds, reptiles and certain mammals that are keratinized structures of epidermal origin (thus belonging to the exoskeleton), and to the mineralized fish 'scales' located within the skin that derive from the dermis (thus belonging to the dermoskeleton). As previously stated, this study deals exclusively with the 'true' dermal scales. However, certain fishes and tetrapods can also present osseous plates formed by the dermis, called osteoderms, that are similar to scales. CASTANET *et al.* (2003) emphasised that there are significant differences between osteoderms and scales and they should not be mistaken. Osteoderms are plates of dermal bone made by intradermal ossification that often bear a pitted outer surface; whereas dermal scales originate from the mesodermal layer of the dermis, are thinner than osteoderms, often round or elongate oval in outline, and may overlap.

Scales, as belonging to the fish skin, are very complex structures, both morphologically and functionally. They assure a series of crucial functions, such as protection or defence, veiling, locomotion, and hydrodynamism (BURDAK, 1979). Scales are a widespread feature of fishes; their reduction or lack of are considered as exceptions and are most often related to odd ecological strategies. Scales are also a useful tool in the study of the fish ontogeny, known as scalimetry. Indeed, the development of scales is modified by the influence of environmental factors and by the growth of the fish in a way that important events in the life-history are recorded on the scale (e.g., CREASER, 1926; OMBREDANE & BAGLINIERE, 1992). It has also been shown that the size of the scale bears a definite relation to the size of the fish at a certain moment of its ontogeny (CREASER, 1926). Scales can regenerate after removal (FRANCILLON-VIEILLOT *et al.*, 1990; ZYLBERBERG *et al.,* 1992).

### V.3.2. DEVELOPMENT AND STRUCTURE

The first stages in the development of a scale are indicated by a fairly distinct and prominent aggregation of mesoderm cells, known as *scleroblasts*, in the upper half of the dermis just below the epidermis. These aggregations form the so-called scale *papillae*, which are separated from the epidermal basal layer cells by a basement membrane, and gradually grow out in a horizontal direction, and in so doing push the epidermis upward. As this stage is reached the cells of the *papillae* arrange themselves in two layers, superior and inferior that will form the superficial and basal portions of the scale, respectively (see above). The different layers of the superficial portion are deposited first and allow an extension in diameter of the scale. Next the basal portion is deposited,

allowing an extension in thickness. The scale bony matrix corresponds to thin irregular layers of a woven-fibred collagenous material.

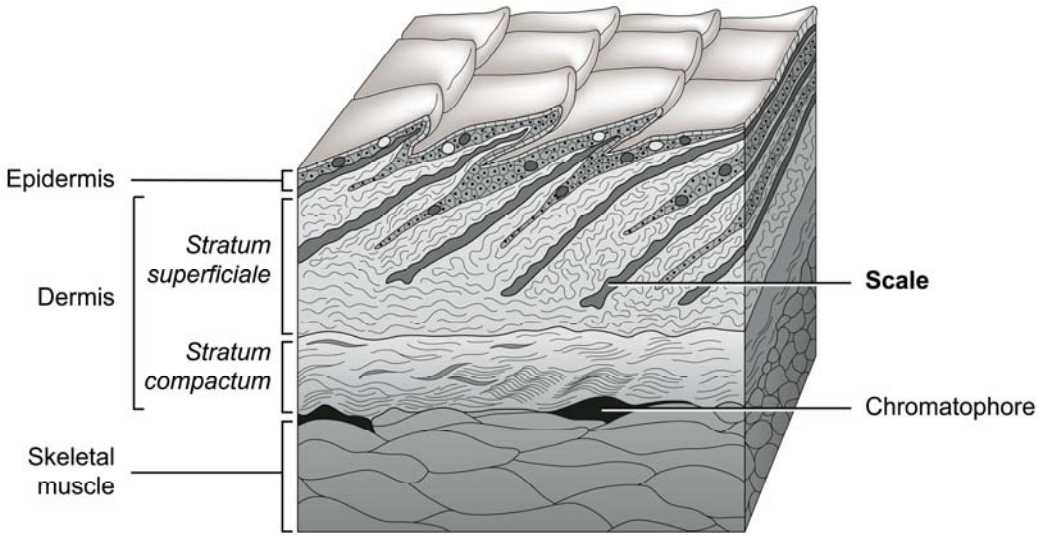



**FIGURE V.3.2.1. Structure of fish skin.** Modified after HELFMAN *et al.,* 2009.

Scleroblasts located near the epidermal-dermal interface can acquire an odontogenic competence. Epithelial cells capping the papillae differentiate into *ameloblasts*, which deposit the enamel matrix in a polarized fashion towards the mesenchyme. The underlying *scleroblasts* differentiate into *odontoblasts* that deposit the dentine matrix. The histological organization and structural identity of the components derived from an odontogenic condensation (e.g., enamel, enameloid, dentine, bone) depend on the timing of the interaction between the mesenchyme of the papilla and the epidermis (SIRE *et al.*, 2009). The same scenario applies to the formation of teeth.

The position of the scale in the dermis begins to change as it increases in size. The posterior end pushes against the epidermis, which it elevates, while the anterior end sinks into the deeper layers of the dermis (CREASER, 1926). The scale pocket is formed, and the scale changes from a horizontal to an oblique position (Fig. V.3.2.1). The basal

layer grows essentially along the internal surface, whereas the superficial layer grows along the external surface. Indeed basal layer growth mirrors that of the superficial layer (OMBREDANE & BAGLINIERE, 1992; SIRE & AKIMENKO, 2004). The core of the scale does not modify its size during growth but house the main processes of bone remodelling (primary and secondary osteones). The outer most part of the spongiosa grows by centrifugal bone deposition, forming the external surface of the scales in non-cosmoid scales. When cosmine is present, the spongiosa forms the overlapped area of the scale. The changes in shape are due to changes in the growth rate of the different fields of the scale, which in turn are partly dependent upon the interference of the growth of one scale with that of another (BAUDELOT, 1873). Scales, except placoid ones, increase in size along with the fish.

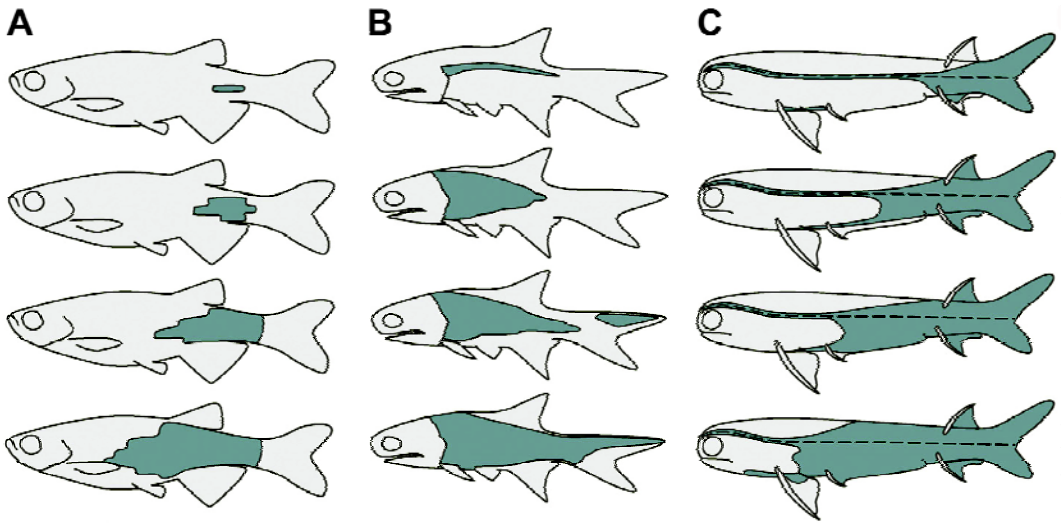



**FIGURE V.3.2.2. Squamation patterns among extant and fossil fishes**. **A.** Extant actinopterygian *Danio rerio*; **B.** Carboniferous actinopterygian *Elonichthys peltigerus*; **C.** Carboniferous "acanthodian" *Acanthodes bridgei*. Ontogenetic changes are from top to bottom. Scale patterns (in green) are mapped on adult outlines. Not to scale. Modified after CLOUTIER, 2010.

The squamation pattern refers to the sequence and position in which scales cover the body during ontogeny. However this pattern and the starting zone of formation of the scales is variable between taxa (Fig. V.3.2.2). Recurrent postero-anterior patterns of squamation along the midline row of scales have been reported in "acanthodians" (ZIDEK, 1985), living chondrichthyans (JOHANSON *et al.*, 2008), and most living actinopterygians (SIRE & AKIMENKO, 2004), suggesting a developmental conservatism, although exceptions exist. However, a more general trend can be identified in vertebrates; scale development usually follows the sensory lines, whether they are lateral as in most osteichthyans or dorso-ventral as in certain heterostracans (GREEMIAUS & WILSON, 2003). The full squamation of the body is considered as an adult criterion (CLOUTIER, 2010).

### V.3.3. DIVERSITY AND EVOLUTION

Fish scales show great polymorphism, depending on their function and the groups where they occur. The main types of fish scales include the scales of chondrichthyans (placoid scales), the scales of early osteichthyans and basal actinopterygians (ganoid scales), the scales of early sarcopterygians (cosmoid scales), and the scales of certain derived sarcopterygians and actinopterygians (elasmoid scales). Although all these scales are evolutionarily linked as derivatives from a common ancestral type (DONOGHUE, 2002) they differ greatly in their morphology and histological structure. Therefore, when referring to the scales of a certain taxon, the type of scale studied should be specified. Here I will detail only the main 'classic' scale types present in osteichthyans, for other scale types of gnathostomes see for instance FRANCILLON-VIEILLOT *et al.* (1990.)

**GANOID SCALE** – Ganoid scales are rhombic in shape and present a well-developed 'peg-and-socket' articulation and Sharpey's fibres anchoring to an internal articular ridge that connects each scale to the adjacent ones. The term ganoid was first applied by AGASSIZ (1833-1844) to describe the 'shiny' scales of certain extant and fossil actinopterygians. The distinction between ganoine and cosmine, the other 'shiny' scale structure, was established by WILLIAMSON (1849). GOODRICH (1907) divided these ganoid scales into the palaeoniscoid and lepidosteoid types.

Palaeoniscoid ganoid scales have three superposed layers: a superficial layer of ganoine (multi-layered enamel), an underlying layer of vascularized dentine (osteodentine), and a basal layer composed of compact lamellar bone (isopedine) (WILLIAMSON, 1849; GOODRICH, 1907; FRANCILLON-VIEILLOT *et al.*, 1990). These scales grow by accretion of ring-shaped peripheral regions with new bone and ganoine layers. Palaeoniscoid scales occur in extinct Chondrostei and in extinct and living Cladistia (e.g. *Polypterus* and *Calamoichthys*).

Lepidosteoid ganoid scales are very similar to the palaeoniscoid scales. Dentine is absent; although early lepisosteids (e.g., *Obaichthys*) retained dentine in their scales (BRITO *et al*., 2000). These scales occur in the extant *Lepisosteus* and *Atractosteus* and in numerous extinct "Holostei".

**COSMOID SCALE** – Cosmoid scales are diagnosed by the presence of cosmine, which is not a tissue but a combination of tissues (enamel and dentine) and a structure (pore-canal system), and are characteristic of sarcopterygians. Usually, cosmoid scales are rhombic, but cosmine can also be present in rounded scales (Paper I). As in ganoid scales, a well-developed 'peg-and-socket' articulation and Sharpey's fibres are primitively present. The term cosmoid scale was first coined by GOODRICH (1907).

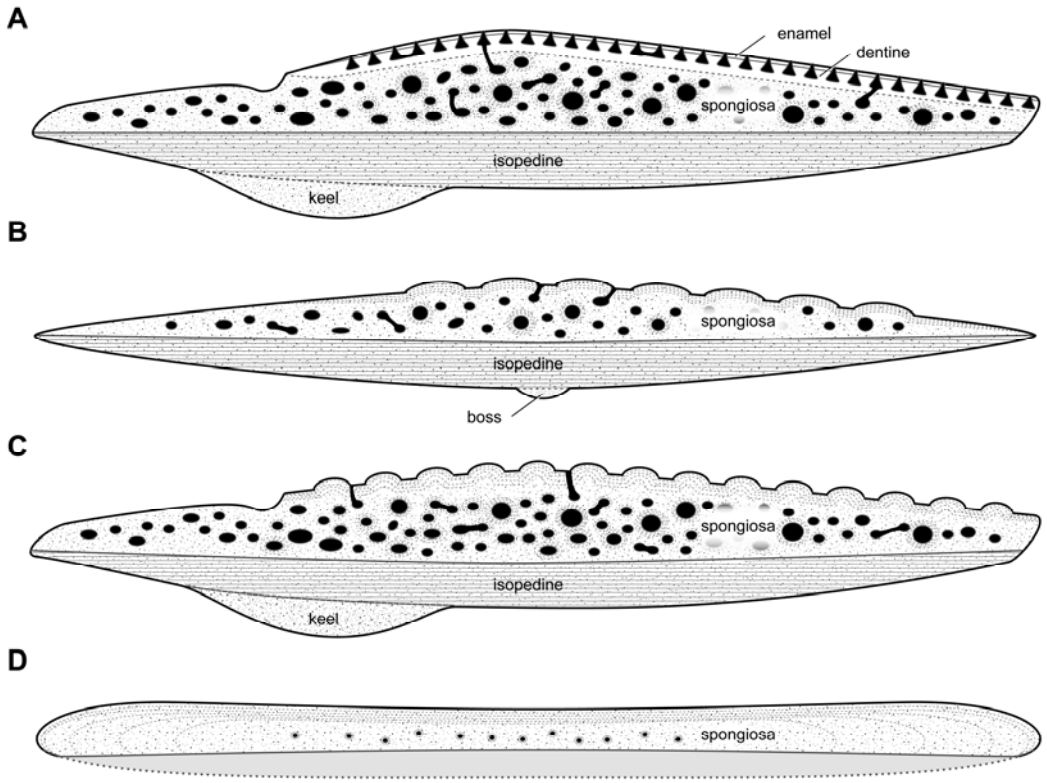



**FIGURE V.3.3.1. Archetypical profile and microstructure of the most-common sarcopterygian scale morphotypes**. **A**. **Primitive rhombic cosmoid scale** as present in porolepiforms (e.g., *Porolepis, Heimenia*), and "osteolepidids" (e.g., *Osteolepis, Gyroptychius*, etc.). Note the presence of the cosmine pores and canals in the enamel and dentine, the thick and well-vascularized spongiosa, the thick isopedine layer, and the internal bony keel. **B**. **Rounded scale** as present in rhizodontids (e.g., *Strepsodus*) and tristichopterids (e.g., *Eusthenopteron*, *Mandageria*, *Cabonnichthys*, etc.). Note the loss of cosmine and its replacement by dense superficial bony ridges, the slightly thinner spongiosa and isopedine layers, and the transformation of the bony keel into a central boss. **C**. **Rhombic cosmine-less scale** as present in "elpistostegalians" (e.g., *Panderichthys*, *Tiktaalik*). Note the absence of cosmine and the presence of dense bony tubercles covering the external surface, the thick and well-vascularized spongiosa, and the retention of a well-defined bony keel under a thick isopedine layer. **D**. **Tetrapod scale** (ovoid, spindle-shaped and/or 'squared') (e.g., *Tulerpeton*, *Greererpeton*, *Plagiosuchus*, etc.). Note the extreme simplification of the scale microstructure with the loss of external ornamentation, the loss of important vascularization in a dense spongiosa, and the loss of the isopedine layer (dashed line). Interpretative drawings based on transversal cross sections along the antero-posterior axis of the scale.

Cosmoid scales comprise three main layers: a superficial layer of cosmine, a middle layer of vascularized bone (spongiosa), and a basal layer of isopedine (GOODRICH, 1907; GROSS, 1956; THOMSON, 1975; Paper I). Under the isopedine, certain scales show a keel made of woven-fibered bone. The cosmine is restricted to the exposed area of the external surface of the scales. The overlapped regions are formed entirely by the spongiosa (superficially) and the isopedine (basally). The cosmoid scale grows in thickness only by the addition of new isopedine lamellae below.

The cosmoid scale forms the basic pattern from which all sarcopterygian scales derive. Structural changes are related to the development or loss of different histological layers (Fig. V.3.3.1). Cosmoid scales occur in the majority of Devonian taxa, but cosmine disappears convergently in almost all groups during the Early to Middle Devonian. Certain groups (e.g., megalichthyid "osteolepiforms") retain cosmine until the Permian. Cosmoid scales are unknown in extant sarcopterygians.

**ELASMOID SCALE** – Elasmoid scales are usually rounded. They show a reduced degree of mineralization and appear thin and transparent. Sharpey's fibres and anchoring devices are absent, although 'attachment fibres' have been described in the external surface of certain cyprinids (ZYLBERBERG & MEUNIER, 1981). Elasmoid scales occur in most actinopterygians (Teleostei and Amiidae), but the scales of the extant sarcopterygians *Latimeria* and dipnoans can also be considered as a particular kind of elasmoid scales (MEUNIER, 1984) (Fig. V.3.3.2).

The elasmoid type was subdivided into cycloid and ctenoid scales by AGASSIZ (1833-44). However, this classification is based only on the presence or absence of comb-like structures or ctenii on the posterior region. Moreover, it has been shown that there is a continuous ontogenetic transition from cycloid to ctenoid scales and both can

occur on the same fish. Recently, elasmoid scales have been subdivided into amioid scales, showing ridges on the overlapped field, and cycloid scales with circuli on the overlapped field (SCHULTZE, 1996b).

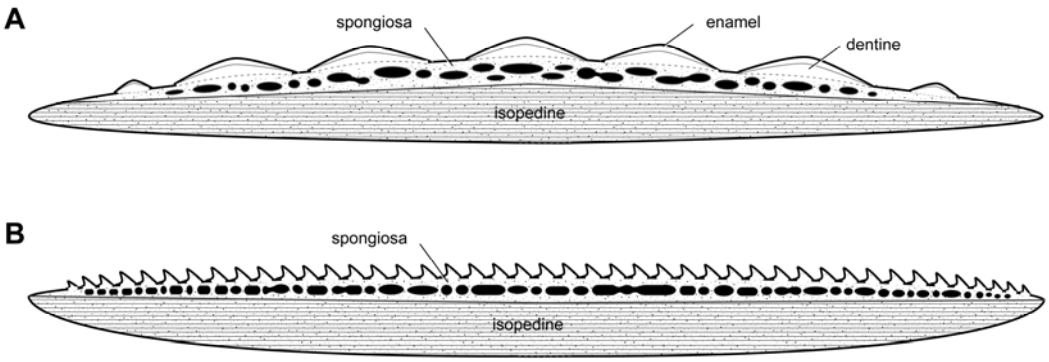



**FIGURE V.3.3.2. Archetypical profile and microstructure of the scales of extant sarcopterygian fishes. A. *Latimeria*** (Actinistia). Note the presence of dentine tubercles capped with enamel (odontodes), the extremely reduced spongiosa and the well-developed isopedine, which is irregularly mineralized. **B. *Neoceratodus*** (Dipnoi). Note the absence of odontogenic components and the reduced 'palisade-like' spongiosa under the minute 'spiny' tubercles of the external surface; the isopedine is extremely thick and, as in *Latimeria*, is irregularly mineralized. Interpretative drawings based on transversal cross sections along the posterior region, orthogonal to the antero-posterior axis of the scale.

Elasmoid scales consist of two main layers: a thick, lamellar, partially mineralized basal layer, covered by a thin, ornamented superficial layer (the so-called external layer). A third layer, the limiting layer, is the most superficial layer to form and is deposited on the external layer, but has a restricted distribution in the posterior field of the scale facing the epidermis (SIRE & AKIMENKO, 2004; SIRE *et al.*, 2009).

Elasmoid scales are characterized by the presence of 'elasmodine', an unmineralized basal layer with a plywood-like structure of the collagen plies (SCHULTZE,

1996b). As previously stated, there is a nomenclatural debate concerning the basal layer of the elasmoid scales (see SCHULTZE, 1996b; SIRE *et al.*, 2009). In this study, I will prefer the term isopedine to elasmodine to describe this unmineralized basal layer of the elasmoid scales (MEUNIER, 1987, 2011).

What do the fossil record and developmental data tell us about the evolution of the scales in osteichthyans? First, that the rhomboid morphotype is the primitive state as evidenced in the stem osteichthyans *Lophosteus* and *Andreolepis* from the Silurian of the Baltic region and Sweden, respectively (GROSS, 1968, 1969, 1971). Cosmoid scales of sarcopterygians and ganoid scales of actinopterygians derive from this morphotype, the main differences between these types being the particular organization of the dentine and enamel (GROSS, 1966).

As previously seen, the rhomboid scale shows a 'peg-and-socket' articulation. Primitively, actinopterygian rhombic scales have a narrow peg and an anterodorsal extended corner, whereas sarcopterygians have a broadly based peg and no extended anterodorsal process. The shape of sarcopterygian rhombic scales appears to be closer to that seen in the basal osteichthyan interlocking system (as in *Lophosteus*). However, the earliest stem sarcopterygians, such as *Guiyu,* show a notable anterodorsal process and a ganoine-like covering of their rhombic scales (ZHU *et al.*, 2009). Similarly, *Meemania* possess the characteristic pores and canal of the cosmine, but shows a series of superimposed odontodes of enamel and dentine, similar to the multi-layered ganoine (ZHU *et al.*, 2006).

These new discoveries blur the 'classic' early separation between sarcopterygians with cosmoid scales and actinopterygians with ganoid scales. The mosaic combination of these features may just reflect a parallel evolution of the rhombic squamation; from an independent trend of enhancing different articulation devices in

primitive osteichthyans, to a transition into rounded scales by secondarily losing these devices in derived actinopterygians and sarcopterygians respectively (CHEN *et al.*, 2012). As a reminder, in this study, rhombic and rounded scale morphotypes refer exclusively to external shape and degree of curbature of the scale margins. A 'rounded scale' should thus not be mistaken with a cycloid elasmoid scale, which can have a very different histological structure.

## V.4. THE FIN RAYS

### V.4.1. FUNCTION

The fin rays belong to the dermal fin skeleton and are one of the key structures related to the success and diversification of fishes enabling diverse morphofunctional adaptations to different habitats and ways of life. Indeed, the dermal fin rays are one of the most important functional elements related to aquatic locomotion (WEBB, 1984, 1988). In fishes, fin rays of both paired and median fins are arranged into a fin web that is the largest flexible and mobile surface of the body. These fin webs are hydrodynamic control surfaces, enhancing trust production and generating off-axis forces during swimming, enabling the fish to develop high manoeuvrability and triggering propulsion (LAUDER & DRUCKER, 2004).

The fin rays provide a flexible structural framework enabling the development of a diversity of behaviours. Some fish use their fins for propulsion, braking, and manoeuvring in the water column. Others also hop, crawl, dig, and hold to the substrate. A number of fishes even use their fins for periods of flight or terrestrial locomotion out of water (TAFT, 2011). This diversity of behaviours is often accompanied by a variety of morphological specializations of the fin rays. Indeed, morphology and bending

properties of the rays themselves contribute significantly to fin function (TAFT, 2011). Thus morphological differences among fin rays are directly related to functional regionalization of the considered paired and/or median fin as a whole. Like the scales, fin rays can also regenerate (AKIMENKO *et al*., 2003).

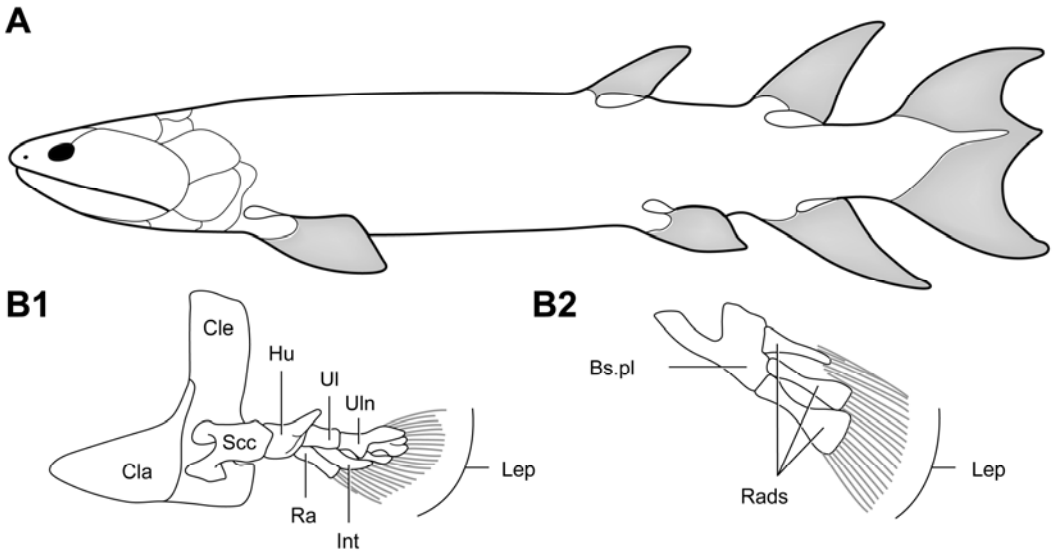



**FIGURE V.4.1.1. Schematic representation of *Eusthenopteron* as a typical sarcopterygian illustrating the distribution and arrangement of the fins rays. A.** Distribution of the fin rays (grey) in the paired and median fins, **B.** Detail of the pectoral fin and girdle (**1**) and of a median fin (e.g., anal) (**2**) showing the articulation pattern of the lepidotrichia with the endoskeletal bones. **Abbreviations**: **Bs**.**pl**, basal plate; **Cla**, clavicle; **Cle**, cleithrum; **Hu**, humerus; **Int**, intermeidium; **Lep**, lepidotrichia; **Ul**, ulna; **Uln**, ulnare; **Ra**, radius; **Rads**, radials; **Scc**, scapulocoracoid. Modified after AHLBERG & JOHANSON, 1998.

### V.4.2. DEVELOPMENT AND STRUCTURE

The different types of fin rays of fishes are gathered under the name dermotrichia (GOODRICH, 1904) in connection to their origin and type of ossification. Among dermotrichia, there are osseous rays, like lepidotrichia and camptotrichia (the

latter, only present in lungfishes), and non-mineralized collagenous rays, such as actinotrichia (in Osteichthyes) and ceratotrichia (in Chondrichthyes). Osteichthyans possess actinotrichia, present in the earliest stages of development and maintained in adults in the most distal part of the fins, and lepidotrichia that form the adult fin web.

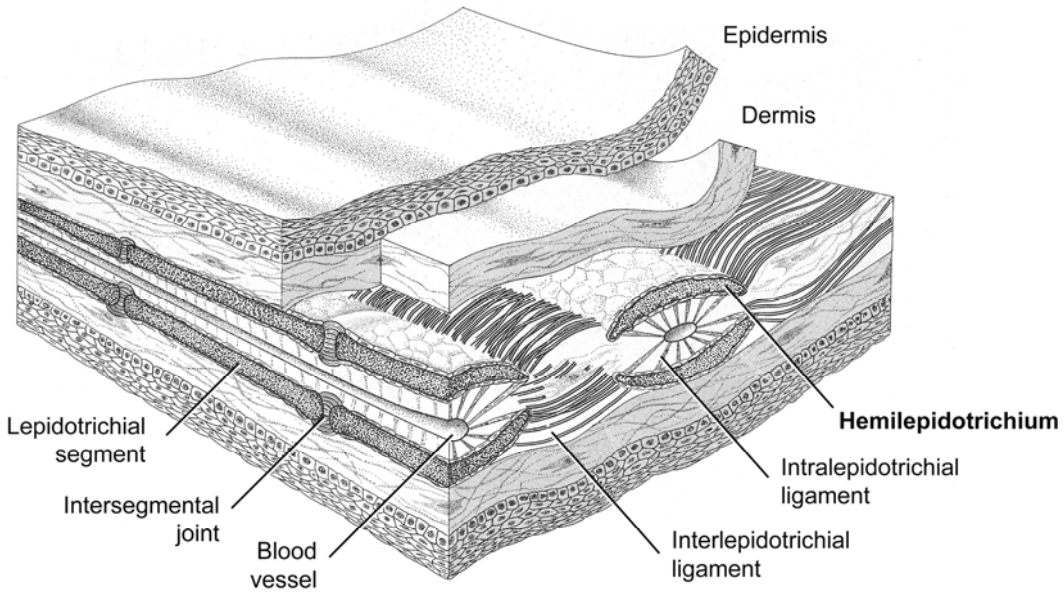



**FIGURE V.4.2.2. Structure of the lepidotrichia in an osteichthyan fin** (e.g., caudal fin). Modified after BECERRA *et al.*, 1983.

Actinotrichia develop in the embryonic fin fold of paired and median fins (ABE *et al.*, 2007. They form the collagenous fin web in the developing larvae until they are replaced by the osseous lepidotrichia. Lepidotrichia form in the basement membrane that separates the epidermis from the underlying mesenchyme. The mesenchymal cells that will form the lepidotrichia use the actinotrichia as a scaffold (FRANÇOIS, 1958; GÉRAUDIE & LANDIS, 1982; SIRE & HUYSSEUNE, 2003). During the formation of the lepidotrichia, actinotrichia are progressively resorbed, both within hemilepidotrichia

and between lepidotrichia, leaving only a narrow distal fringe in the adult fins of the majority of osteichthyans.

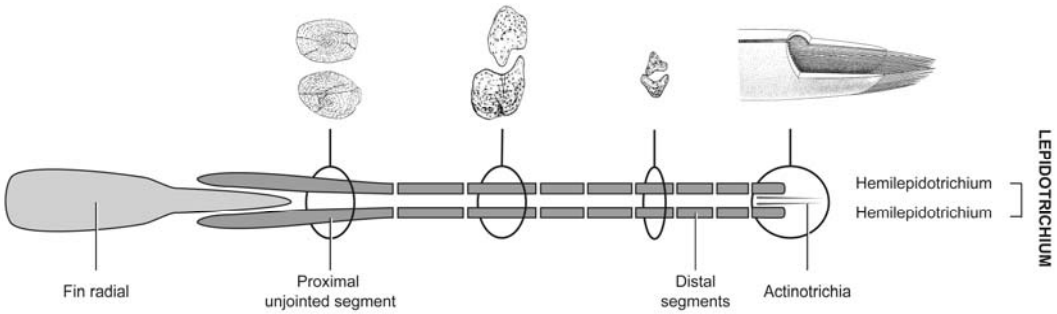



**FIGURE V.4.2.3. Schematical representation of the archetypical morphology of a lepidotrichium.** Redrawn and modified after GOODRICH, 1904; BECERRA *et al.,* 1983; JEFFERY, 2001.

Each lepidotrichium is composed of two parallel and symmetrical bony elements in the shape of a parenthesis (i.e., hemilepidotrichium). Lepidotrichia are segmented (i.e., formed by a series of repetitive articulating elements separated by joints) and distally bifurcated (the distal portion of the ray is split) (Fig. V.4.2.3). The most proximal portion is always unjointed and articulates with the radial bones of the fins. Segmentation and bifurcation are independent processes, regulated by different genes, but they are related during development (MARÍ-BEFFA & MURCIANO, 2010). The camptotrichia of dipnoans derive from lepidotrichia and consist of partially ossified fin rays in which the inner portion of the ray remains in a collagenous state (GÉRAUDIE & MEUNIER, 1982, 1984).

### V.4.3. DIVERSITY AND EVOLUTION

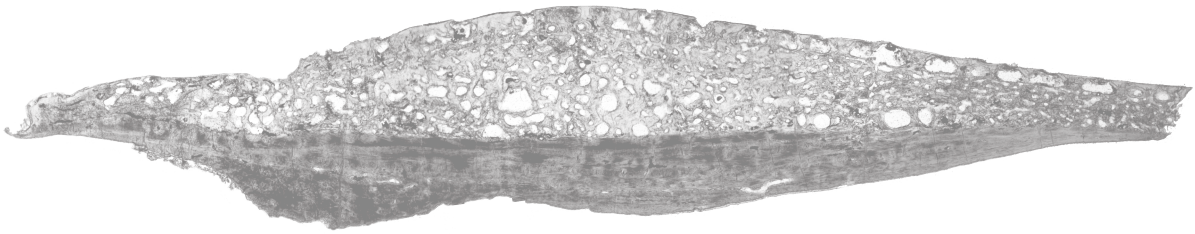
Although lepidotrichia are the main type of fin rays found in fossil specimens, they have attracted little attention of researchers, since it was considered that once they were established in osteichthyans they were minimally modified during the evolution of the group. However, a closer look at their structure and histology reveals that lepidotrichia experienced a series of morphological changes in almost all groups of osteichthyans, and eventually played a capital role during the fish-tetrapod transition.

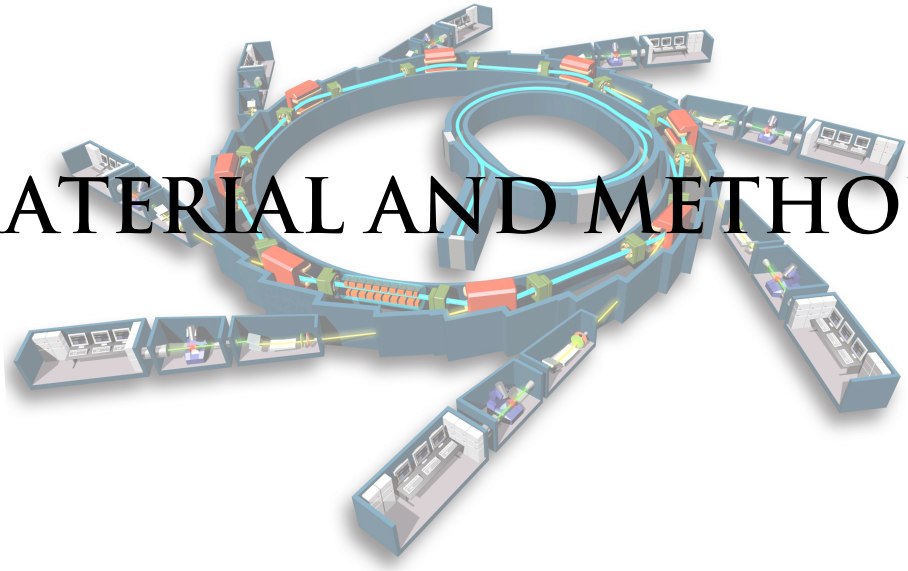
During sarcopterygian evolution, a large set of fin ray morphologies arose from a primitive and stable osteichthyan condition of segmented and branched lepidotrichia (SCHAEFFER, 1968). Certain groups develop unbranched rays (e.g., coelacanths, extant lungfishes), whereas others distalize segmentation (e.g., rhizodontids and "elpistostegalians"). In sarcopterygians, the distalization of segmentation produced the lengthening of the proximal unjointed portion and could be associated with the distal proliferation of the fin endoskeleton, and considerable overlap between the proximal lepidotrichia and the proliferating endoskeleton (DAESCHLER & SHUBIN, 1998; DAESCHLER *et al.*, 2006; SHUBIN *et al.*, 2006). In Devonian tetrapods, such as *Acanthostega*, lepidotrichia of the caudal fin are totally unsegmented (COATES, 1996). After the Devonian, fin rays disappear completely from the fins of tetrapods (further information on fin ray structure, development, and evolution can be found in Paper IV).

## VI. AIM OF THE STUDY

The Devonian was a period of major transformations for life on Earth. The relationships between bio- and geosphere changed forever with the transition to land of plants, and later of vertebrates. Sarcopterygian fishes diversified in the sea and in fresh waters throughout the Devonian. Global environmental changes certainly influenced their anatomical and physiological evolution and allowed (or prevent) their paleogeographic dispersion. Somewhere during the Middle to Late Devonian, tetrapods evolved from a stock of tetrapodomorph fishes, grew limbs with digits, and initiated the first stage of the transition to land. However, these early tetrapods were still aquatic animals that retained several primitive 'fish-like' features, the more evident were a scale covering and a tail supported by fin rays. Scales and fin rays also evolved during the transition from fishes to tetrapods, and would be eventually lost later during the 'terrestrialization' process. However, several aspects of the evolutionary modifications that took place during the transition to land of vertebrates, as well as the morphofunctional and physiological role that these features played in the way of life of early tetrapods, are still unclear.

The main aim of this thesis is thus to study the morphological and developmental changes of the scales and fin rays in sarcopterygians in order to better understand the 'fish-tetrapod transition'. In order to do so, I shall deal with a diverse set of data and methodologies that will enable me to study crucial aspects of their fine microstructure, growth patterns, and development. Observations on fossil sarcopterygians, anatomical comparisons and experimental manipulation with extant fishes will provide the framework for the proposition of hypothesis and the identification of trends in the evolution of the dermoskeleton in vertebrates, in general, and in tetrapods, in particular.





# MATERIAL AND METHODS

Paper I
www.synchrtron-soleil.fr
DAVIS et al., 2004b

# I. MATERIAL

During the course of this research, I had the opportunity to examine material from very different sources, comprising both fossil and living fish specimens. Most of the fossil material examined is housed at the Muséum National d'Histoire Naturelle (MNHN) in Paris. I also had the chance to study complementary material housed in various foreign institutions during a series of short stays in the Museum für Naturkunde (MB) in Berlin, the Academy of Natural Sciences Philadelphia (ANSP) in USA, the Uppsala University (UP) in Sweden, and the Málaga University (UMA) in Spain.

I will detail here all the fossil and living material that I have studied, handled, sectioned, and/or figured in the course of this thesis. Collection numbers and location of origin of the specimens will be given for the sectioned and/or figured material only. Acquisitions (e.g., cross sections, drawing, etc.) and references to figures will also be detailed.

Concerning the studied fossil and living material, and due to the often large number of specimens for a single species or genus held in the formerly cited collections, I will solely detail the taxonomic attribution (genus and species), the institution where the material is housed (e.g., MB, ANSP, etc.), and the city where this material was studied (e.g., Berlin). When the material-housing institution differs from the city where the material was studied it implies that the material was temporarily loaned to visited institution. For a complete list of institutional abbreviations see the Appendices.

Finally, a special emphasis will be given to the zebrafish (*Danio rerio*) due to his importance as a model organism in developmental biology studies. In this section I will describe key aspects of its biology and development and highlight the reason of its current position as 'Model organism' for the study of vertebrate development.

## I.1. STUDIED MATERIAL

### I.1.1. FOSSIL MATERIAL

#### I.1.1.1. SECTIONED AND/OR FIGURED MATERIAL

**DIPNOMORPHA**

**Porolepiformes**

| | |
|---|---|
| *Porolepis sp.* | Early Devonian of Spitsbergen (Norway)<br>Isolated scales (MNHN.f. SVD 4217), base of a dorsal fin and nearly complete caudal fin (MNHN.f. SVD 4319 A/B).<br>Drawings (Paper IV) and synchrotron microtomographic acquisitions (in prep.). |
| *Heimenia ensis* | Early-Middle Devonian of Spitsbergen (Norway)<br>Nearly complete body (LIG 45–2027), tooth cross sections (LIG 45–2019), and isolated scales (LIG 45 – 2018 – 2042).<br>Cross sections of six scales (Paper I) and a tooth (Paper II). |
| *Holoptychius sp.* | Late Devonian of Latvia<br>Isolated tooth (MB.f. 2129,4), scales (MB.f. 1991.2, 1994.1,2).<br>Cross sections of three scales (including a lateral line scale) and a tooth (Paper II). |
| *Laccognathus panderi* | Middle Devonian of Latvia<br>Isolated teeth (MB.f. 1849, 1850), scales (MB.f. 1833.2,6,13).<br>Cross sections of three scales (including a lateral line scale) and a tooth (Paper II). |

**Dipnoi**

| | |
|---|---|
| *Dipterus valenciennesi* | Middle Devonian of Achanarras (Scotland)<br>Well-preserved complete bodies (MNHN.f. GBP 386)<br>Figured (Paper IV). |
| *Scaumenacia curta* | Late Devonian of Miguasha (Québec, Canada)<br>Well-preserved complete body (MNHN.f. 1968.9) and caudal fin (MNHN.f. 1968.8.2 a/b).<br>Figured (Paper IV). |

**TETRAPODOMORPHA**

"**Osteolepiformes**"

| | |
|---|---|
| *Osteolepis macrolepidotus* | Middle Devonian of Achanarras (Scotland)<br>Well preserved complete bodies (MB.f. 5196, 5425).<br>Cross sections of skulls, fins and scales (in prep.). |

| | |
|---|---|
| *Gyroptychius agassizi* | Middle Devonian of Achanarras (Scotland) |
| | Well preserved posterior portion of the body (MB.f. 5195.b). |
| | Cross sections of fins and scales (in prep.). |
| *Megalichthys hibberti* | Late Devonian of Red Hill (Pennsylvania, USA) |
| | Isolated scales (ANSP Field Crew 2009). |
| | Cross sections and microtomographic acquisitions (in prep.). |
| *Hyneria lindae* | Late Devonian of Red Hill (Pennsylvania, USA) |
| | Isolated tooth (ANSP Field Crew 2009). |
| | Cross sections and microtomographic acquisitions (in prep.). |
| Rhizodontid indet. ANSP | Late Devonian of Red Hill (Pennsylvania, USA) |
| | Complete body, squamation and caudal fin (ANSP 21334-8) |
| | Figured (in prep.) |
| "**Elpistostegalia**" | |
| *Panderichthys rhombolepis* | Late Devonian of Montsevo (Russia) |
| | Isolated scales (PIN, unnumbered). |
| | Cross sections and microtomographic acquisitions (in prep.). |
| **Tetrapoda** | |
| *Tulerpeton curtum* | Late Devonian of Tula (Russia) |
| | Isolated scales (PIN 2921/3238, 3239). |
| | Cross sections, microtomographic acquisitions (Paper III). |

#### I.1.1.2. STUDIED FOSSIL MATERIAL FOR COMPARISONS

| | |
|---|---|
| **Stem Sarcopterygii** | |
| *Psarolepis romeri* | Isolated scales. IVPP, Uppsala. |
| **Onychodontida** | |
| *Grossius aragonensis* | Complete skull. GO, Berlin. |
| *Onychodus jaeckeli* | Skull bones and scale fragments. MB, Berlin. |
| *Onychodus sigmoides* | Isolated teeth. MB, Berlin. |
| *Strunius walteri* | Complete body, scales and lower jaw fragments. MB, Berlin. |
| **Actinistia** | |
| *Rhabdoderma elegans* | Complete bodies, caudal fin, and scales. MB, Berlin. |
| *Coelacanthus granulatus* | Complete bodies and isolated caudal fin. MB, Berlin. |
| *Diplocercides kayseri* | Complete bodies. MB, Berlin. |
| *Undina penicillata* | Complete bodies and caudal fin. MB, Berlin. |
| *Macropomoides orientalis* | Complete bodies. MB, Berlin. |
| *Swenzia latimerae* | Complete body. MNHN, Paris. |

**DIPNOMORPHA**

**Porolepiformes**

| | |
|---|---|
| *Porolepis sp.* | Complete bodies, isolated scales and teeth. MNHN, Paris. |
| *Heimenia ensis* | Complete body, isolated scales and teeth. LIG, Paris. |
| *Holoptychius americanus* | Isolated scales. ANSP, Philadelphia. |
| *Holoptychius nobilissimus* | Isolated scales. MB, Berlin. |
| *Holoptychius giganteus* | Isolated teeth and scales. ANSP, Philadelphia and MB, Berlin. |
| *Holoptychius flemingii* | Complete bodies. MB, Berlin. |
| *Laccognathus panderi* | Lower jaws and isolated teeth and scales. MB, Berlin. |
| *Laccognathus embryi* | Lower jaws, isolated teeth and scales. ANSP, Philadelphia. |
| *Ventalepis ketleriensis* | Isolated scales. MB, Berlin. |
| *Glyptolepis baltica* | Isolated scales. MB, Berlin. |
| *Glyptolepis leptopterus* | Complete bodies. MB, Berlin. |
| *Hamodus* sp. | Isolated teeth. MB, Berlin. |

**Dipnoi**

| | |
|---|---|
| *Dipterus valenciennesi* | Complete bodies. MB, Berlin and MNHN, Paris. |
| *Rhinodipterus ulrichi* | Complete bodies and isolated scales. MB, Berlin. |
| *Chirodipterus* sp. | Complete bodies. MB, Berlin. |
| *Scaumenacia curta* | Complete bodies. MB, Berlin and MNHN, Paris. |
| *Conchopoma gadiforme* | Complete bodies. MB, Berlin. |

**TETRAPODOMORPHA**

**Rhizodontida**

| | |
|---|---|
| *Rhizodus hibberti* | Fin and jaw fragments, isolated teeth and scales. MB, Berlin. |
| *Rhizodus ornatus* | Isolated teeth and scales. MB, Berlin. |
| *Strepsodus sauroides* | Isolated teeth and scales. MB, Berlin. |
| Rhizodontid indet. ANSP. | Complete body. ANSP, Philadelphia. |

"**Osteolepiformes**"

| | |
|---|---|
| *Megalichthys hibberti* | Isolated scales. ANSP, Philadelphia and MB, Berlin. |
| *Litoptychus bryanti* | Isolated scales. ANSP, Philadelphia. |
| *Eusthenopteron foordi* | Complete bodies. MB, Berlin. |
| *Jarvikina wenjukovi* | Isolated teeth. MB, Berlin. |
| *Latvius grewingki* | Isolated scales. MB, Berlin. |
| *Osteolepis macrolepidotus* | Complete bodies. MB, Berlin. |
| *Osteolepis panderi* | Complete bodies. MB, Berlin. |
| *Gyroptychius agassizi* | Complete bodies. MB, Berlin. |
| *Gyroptychius milleri* | Complete bodies. MB, Berlin. |
| *Rhizodopsis sauroides* | Complete bodies. MB, Berlin. |

| | |
|---|---|
| *Rhizodopsis hanbuchi* | Complete bodies. MB, Berlin. |
| *Glyptopomus bystrowi* | Isolated scales. MB, Berlin. |
| *Tristichopterus alatus* | Complete bodies and caudal fin. NMS, Uppsala; MNHN, Paris. |
| *Spodichthys buetleri* | Lower jaws and skull fragments. MGUH, Uppsala. |
| *Hyneria lindae* | Fin fragments, isolated teeth and scales. ANSP, Philadelphia. |
| Tristichopterid indet. ANSP. | Lower jaws and skull fragments. ANSP, Philadelphia. |

"**Elpistostegalia**"

| | |
|---|---|
| *Panderichthys rhombolepis* | Lower jaw fragments and isolated scales. MB, Berlin. |
| *Tiktaalik roseae* | Nearly complete body and lower jaws. ANSP, Philadelphia. |

**Tetrapoda**

| | |
|---|---|
| *Tulerpeton curtum* | Isolated scales. PIN, Paris. |

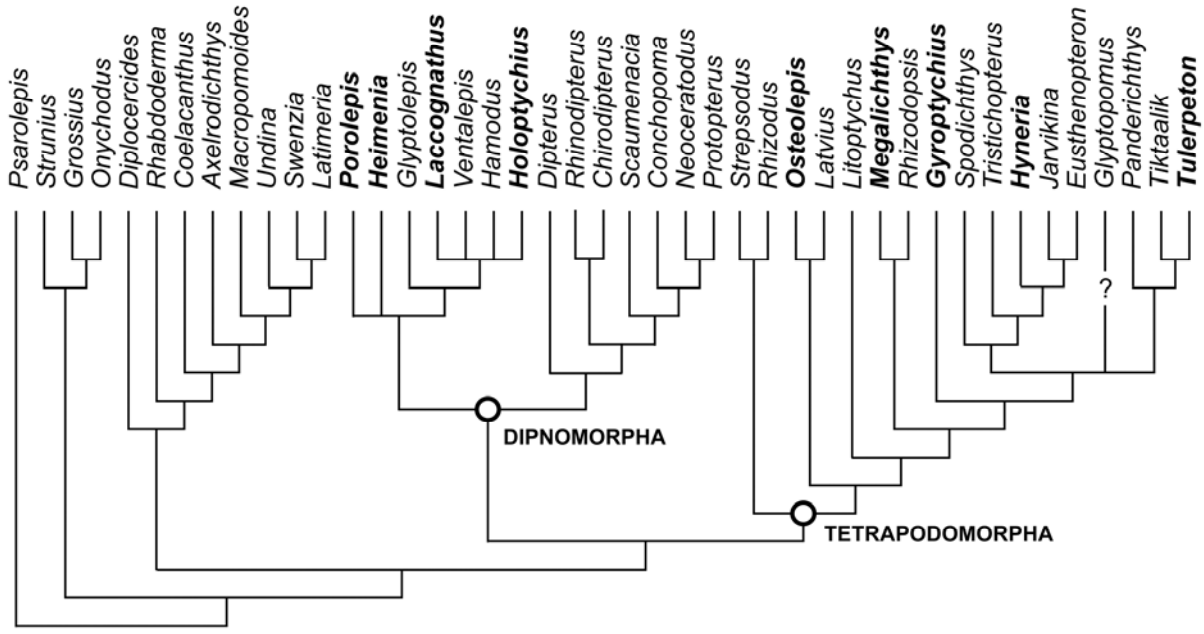



**FIGURE I.1.1.1. Consensual cladogram of sarcopterygian interrelationships illustrating the genera studied in this thesis.** Genera in bold correspond to sectioned and/or figured material. Phylogenetic hypothesis after JANVIER, 1996; AHLBERG & JOHANSON, 1998; CLÉMENT, 2001; SCHULTZE, 2004; SNITTING, 2008a,b; COATES *et al.*, 2008; LU & ZHU, 2010, and QIAO & ZHU, 2009.

### I.1.2. LIVING MATERIAL

#### I.1.2.1. STUDIED LIVING MATERIAL FOR COMPARISONS

| | |
|---|---|
| **SARCOPTERYGII** | |
| **Actinistia** | |
| *Latimeria chalumnae* | Complete bodies (adults) and isolated scales. MNHN, Paris. |
| **Dipnoi** | |
| *Protopterus annectens* | Complete bodies (juveniles and adults). MNHN, Paris. |
| *Neoceratodus forsteri* | Complete bodies (adults) and isolated scales. MNHN, Paris. |
| **ACTINOPTERYGII** | |
| **Cladistia** | |
| *Polypterus senegalensis* | Complete bodies (adults) and isolated scales. MNHN, Paris. |
| **Ginglymodi** | |
| *Lepisosteus osseus* | Complete bodies (adults) and isolated scales. MNHN, Paris. |
| **Teleostei** | |
| *Danio rerio* | Complete bodies (larvae, juveniles and adults). UMA, Málaga. |

## I.2. THE ZEBRAFISH

The zebrafish (*Danio rerio* HAMILTON-BUCHANAN 1822) is an actinopterygian fish, member of the Ciprinidae family of the order Cipriniformes, close to minnows and carps. It is a tropical freshwater fish that arose in the Ganges region, Eastern India. In its natural environment it commonly inhabits streams, canals, ditches, ponds, and slow-moving to stagnant waters, including rice fields. It is a popular aquarium fish and it has become of common use in scientific research.

The zebrafish possess five to nine uniform, pigmented, horizontal dark blue stripes on both sides of the body, all of which extend from behind the operculum to the end of the caudal fin (Fig. I.2.1). This peculiar coloration pattern, similar to that of a zebra, gives its name to this fish. Its shape is fusiform and laterally compressed, with the

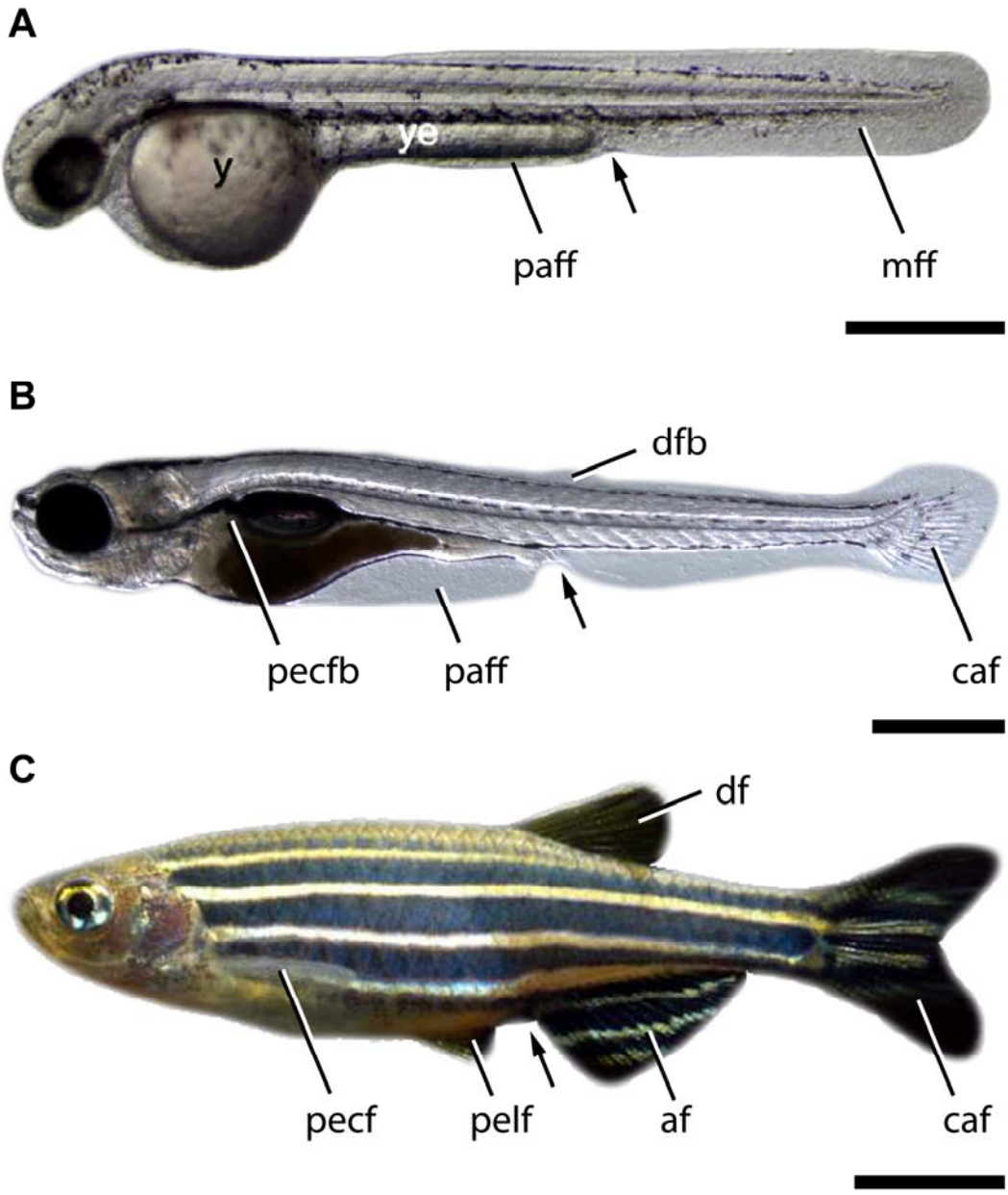



**FIGURE I.2.1. Main stages of the ontogenetic development of the zebrafish (*Danio rerio*)**. **A.** Zebrafish embryo (42 hpf), overview of the median fin fold. Scale bar equals 500 μm (modified after ABE *et al.*, 2007). **B.** Juvenile zebrafish (around 15 dpf), overview of the pectoral and dorsal fin buds and formation of the hypurals and lepidotrichia in the caudal fin. Scale bar equals 500 μm **C**. Adult zebrafish, overview of the paired and median fin pattern. Scale bar equals 10 mm. Arrow in A, B, C points the anus. **Abbreviations**: **af**, anal fin; **df**, dorsal fin; **dfb**, dorsal fin bud; **caf**, caudal fin; **mff**, median fin fold; **paff**, preanal fin fold; **pecf**; pectoral fin; **pecfb**; pectoral fin bud; **pelf**, pelvic fin; **y**, yolk sac; **ye**, yolk sac extension.

mouth directed upwards. As many other actinopterygians, it possesses three median fins: a dorsal, an anal and a caudal fin; and two sets of paired fins (pectoral and pelvic).

The zebrafish can grow up to 6.4 centimetres. Life span in captivity is around 2 to 3 years but in ideal conditions it may extend to 5 years. External habitat temperature is ideally 28.5 °C for a normal development. Males are smaller than females but they differ by the presence of dermic spiculae on male lepidotrichia that give to pectoral fins a more brown coloration, whereas females translucent pectoral fins lack those spiculae.

*Danio rerio* has become a key component in our understanding of vertebrate development and has gradually acquires the rank of Model Organism (KIMMEL *et al.*, 1995; METSCHER & AHLBERG, 1999) for several reasons:

- Easy to keep in the lab due to its small size
- Extremely fertile (a female can produce up to 200 eggs in a week)
- Short generation time (fertile adults are generated in less than 3 months)
- Development progresses rapidly (most of the organs are formed within 24 hours and completely formed individuals are viable only 48 hpf, hours post fertilization)
- Breeds readily (swimming and feeding behaviour begin about 36 hph, hours post hatching)
- Produces conveniently transparent embryos (which enable to observe and experience with any embryonic phase)
- The genome has been completely sequenced (it presents a 80% of homologous genes with those of humans)
- Possesses the capacity to regenerate part of its organs (such as fins, heart, optic nerve and dorsal spine, among others)

Genetic analysis of zebrafish fin buds has shown that the signalling interactions and gene networks that control fin bud development are conserved with tetrapods (e.g., MERCADER, 2007). Such studies have begun to show the molecular alterations that might underlie the fin to limb transition during vertebrate evolution, thus justifying the use of the zebrafish in evo-devo studies on the early evolution of tetrapods.

# II. METHODS

Different methodologies have been used in this thesis in order to obtain the maximum amount of information from the material. Due to the pluridisciplinary aim of the research, each methodology was adapted to the material at hand. Fossil material was studied by means of 'classic' and new histological and imaging techniques that revealed the internal structure of osseous dermal components, whereas extant fishes were raised and treated in the laboratory to attempt the description of their development.

Here I will detail these different techniques, highlighting their advantages and disadvantages, and the problems I had to deal with. Each description will be preceded by a short historical revision of their development.

## II.1. CROSS SECTIONS

### II.1.1. HISTORICAL CONTEXT

GOODRICH (1913) was the first to use the term "palaeohistology" (from the Greek "palaios" = old, "histos" = fabric, and "logos" = word, speech) to designate the study of mineralized tissues of fossil organisms (RICQLÈS *et al.*, 2004). Earlier, OWEN (1840-1845), WILLIAMSON (1849), and PANDER (1860) were among the first to publish studies on animal palaeohistology. OWEN focused on the teeth of reptiles, whereas WILLIAMSON and PANDER studied fish teeth and scales of fossil sarcopterygians and actinopterygians in order to better understand their development. These early works established the classical scale taxonomy (e.g., ganoid, placoid, and cosmoid scales) of different fossil groups made formal by AGASSIZ (1833-1844).

Palaeohistology evolved in the twentieth century with the appearance of the so-called Swedish and German schools (JANVIER, 1996). In the Swedish school, STENSIÖ, but more particularly ØRVIG, developed a biological approach based on the observation of bone microstructure among early vertebrates (e.g., heterostracans, placoderms, chondrichthyans) and theorized on the evolution of hard tissues (e.g., the odontode and lepidomorial theory) (ØRVIG, 1977; DONOGHUE, 2002). In the German school, GROSS (1936) became interested in the identification of specialized mineralized tissue in some groups with under a primary taxonomical approach setting the bases of what became known as comparative palaeohistology.

Finally, very recently, the study of bone microstructure entered on a new dimension with the emergence of new technologies based on microtomographic scanning (e.g., CT-scanning, synchrotron light) that enable to observe micron and submicron structures of fossil tissues in three dimensions without damaging them. Since the establishment of the these techniques as a powerful tool for the study of the internal microstructure of fossil hard tissues (TAFFOREAU *et al.*, 2006; TAFFOREAU & SMITH, 2008; SANCHEZ *et al*., 2012), the field of palaeohistology has experienced a renaissance offering a whole new set of scientific possibilities (see below).

### II.1.2. CROSS SECTION PROTOCOL

All histological data presented in this thesis come from microscopic observations of thin sections made on fossil material. Lilian CAZES (UMR 7207, MNHN) performed 17 thin sections (see Papers I, II, III) and introduced me to the 'standard' protocol of implementation of thin cross sections on paleontological material (CHIMSANY & RAATH, 1992), which I shall briefly detail here.

**1. Inclusion of fossil specimens**

Fossil specimens (e.g., scales, teeth, bones, etc.) are embedded in a liquid resin that slowly penetrates the microscopic spaces. The complete inclusion in the resin takes about one week. The time span of the inclusion is rather long, but it is better for the fossil material that the resin impregnation is slow and gradual. Indeed, a quick impregnation time can damage the internal structure of the samples and may even lead to internal fractures of the fossil material. Once the resin has dried out it becomes possible to manipulate the samples and to define more accurately the cutting planes.

**2. Cutting the specimens**

The specimens (now in the form of small cubes of harden resin) are cut using a diamond wire saw. The cut is made along previously determined cutting planes, chosen accordingly to their scientific interest. The use of a wire saw has been preferred instead of that of a disk saw in order to minimize material losses. The cutting can take several hours, depending on the size of the specimens.

**3. Preparation of the cut surface and gluing to the glass slide**

Once the samples are cut into thin slices, the resulting cut surface of each slice must be treated in order to be attached to a glass slide. The surface is worn on a wet plate covered with an abrasive powder (silicium carbide). Powder grains with a diameter of 3 µm are suitable to homogenize and clear the surface irregularities. After that, the treated surface is polished with a velvet disk coated with a suspension aluminium oxide (alumina powder). The sample is then glued to a glass slide (of according size to the fossil specimen) using a resin (Araldite) on a 40°C hot plate for 48 hours.

**4. Rectification of the cutting thickness**

After gluing the fossil material to the glass slide, the portion of the sample that exceeds in height must be cut. The cut is again performed with a saw cut diamond wire, as close

as possible to the glass slide. Then, the thin section is inserted into a "grinder" machine that will slowly thin the sample using a rotating diamond wheel. The general thickness of the section can then be set. The thickness of a thin section depends on the surface of the specimen and on the desired histological observations to be made. The thickness of the samples studied in this thesis ranges from around 40 µm to 25 µm. To finalize the thinning of the thin section, the sample is again worn with abrasives of different grain size and then polished. This last polishing will enable to better appreciate the histological structures under a microscope. Throughout the process, it is possible to observe the thin sections under a microscope and correct the progress of worn. A uniform wearing will allow clearer observation of the histological structures.

**5. Covering the thin section**

Once the desired observation thickness is obtained, the glass slide containing the sample is covered with a thin glass coverslip. The specimen number is noted on the glass slide before the covering. Slide and coverslip are bonded with a resin (Araldite) on a 40°C hotplate for 48 hours. After that, the cross sections are ready to handle and study.

## II.2. X-RAY MICROTOMOGRAPHY

### II.2.1. HISTORICAL CONTEXT

The varied nature of fossil specimens makes it extremely difficult to study the internal anatomy and microstructure of their osseous component without destroying them. This is particularly true for palaeohistology as previously described, a technique that although being extremely informative requires the partial or total destruction of the fossil material. The use of X-ray imaging to the study of fossil specimens has not only enable to visualize the internal structure of bones but also to virtually reconstruct the

three dimensional arrangement of hidden structures and tissues thanks to powerful imaging softwares (e.g., Materialise Mimics®, Volume Graphics VG Studio Max®). The development of these new techniques has dramatically broaden our field of observation and a whole new amount of microstructural, cytological, and even vascular data is slowly emerging from the deepens of bones (SANCHEZ *et al.*, 2012).

Before the application of the non-destructive X-ray microtomography, a series of destructive techniques were developed at the beginning of the twentieth century to study the internal structure of fossil vertebrates. SOLLAS (1903) was the first palaeontologist to use the technique of polishing series in his study of the enigmatic *Palaeospondylus* from the Late Devonian of Scotland (SOLLAS & SOLLAS 1903). The method of polishing series consisted of the cutting of the fossil specimens in slices of several micrometres to several millimetres in thickness. Each cutting surface was then polished and photographed. Images were processed in order to enlarge them and reconstruct the internal anatomy by drawing or sculpting in wax plates. The plates were finally assembled and glued to each other to recover an enlarged three-dimensional model of the specimen.

The Swedish School led by STENSIÖ (1927) developed this technique in his study of the osteostracan cephalaspids from the Early Devonian of Spitsbergen, and JARVIK (1954) took it a step further in his classical study of the skull of *Eusthenopteron* from the Late Devonian of Miguasha (Québec, Canada) by gridding series (JARVIK, 1980 and references therein). Similar applications have since been conducted by POPLIN (1974) in her study of the braincase of actinopterygians from the Carboniferous of USA, by JANVIER (1981) in his study of the vestibular chamber of the cephalaspid *Norselaspis glacialis* from the Lower Devonian of Spitsbergen, and by CHANG (1982) in her study of the braincase of the stem dipnomorph *Youngolepis* from the Early Devonian of China.

Unfortunately, the method of polishing series presents two major disadvantages: first, the fossil is completely destroyed after the polishing phase, and second, it requires an extremely important amount of time (JARVIK and his two technicians spent almost 12 years in the completion of the wax model of *Eusthenopteron*!).

In the 1990's, the more and more common use of medical X-ray tomography draw the attention of palaeontologists and anatomists that saw the opportunity to visualize the internal structure of extant or fossil organisms without damaging them. CLOUTIER *et al.* (1988), SCHULTZE (1991), and SCHULTZE and CLOUTIER (1991) were among the first to use CT-scanning techniques to study the anatomy of sarcopterygian fishes focusing in the cranial and postcranial anatomy of the extant coelacanth *Latimeria.* From this point on, X-ray microtomography became a very popular tool in palaeontology and hasn't stopped developing until today. Now a large set of available X-ray techniques (e.g., Magnetic Resonance Imaging, CT-scanning, Synchrotron scanning) can be used to study different aspects of the internal anatomy of key organisms, from visceral arrangement in extant taxa (MRI, CT-scanning), to bone composition and microstructure in fossils, and even cell distribution (Synchrotron scanning).

### II.2.2. MICROTOMOGRAPHICAL TOOLS

#### II.2.2.1. CT-SCANNING

X-ray computed tomography, also known as CT-scanning, is a medical imaging procedure measuring the X-ray absorption of the tissues from specific body areas in order to reconstruct 2D or 3D images of the anatomical structures of interest. A beam of X-rays is generated from an X-ray source. The sample is located on a rotative platform that rotates the object 360° along the Y-axis between the beam and an array detector. X-

ray sensors in the array detector perceive and measure the radiance intensity after the partial absorption of the X-rays by the specimen. The digital images taken along 360° (the so-called projections) are then processed by a computer, which assigns to each pixel a grey-scale value that is proportional to the X-ray absorbance of each part of the structure of interest.

These projections enable to retrieve a 'radiographic volume' from which virtual 'slices' are then reconstructed (ranging from several hundred to several thousands) in XY, XZ and YZ stacks by high-performance computer(s). Each virtual slice is composed of '3D pixels', the so-called voxels (pixels with x, y and z dimensions): the size of these voxels gives the inter-slice spacing or the 'virtual thickness' of the slice. The voxel size also corresponds to the resolution of the scan and in consequence a thin inter-slice space would reveal more details than a thick one, but would also produce larger data sets. The tomographic slices can be treated with various tomographic reconstruction softwares (Materialise Mimics®, Volume Graphics VG Studio Max®, VSG AVIZO®, etc.). These softwares allow the segmentation of a region of interest in every spatial plane (sagittal, axial, coronal and oblique) and the calculation of a 3D model.

CT-scan microtomographic data were obtained in Paris from the newly acquired CT-scan of the 'AST-RX' platform (UMS CNRS/MNHN 2700) of the MNHN. Miguel GARCÍA SANZ (UMS 2700, MNHN) performed the microtomographic acquisitions and Florent GOUSSARD (UMR 7202, MNHN) supplied the logistic and initial formation to the virtual reconstruction in the 'Paleontology Imaging Unit' (UMR CNRS/MNHN/UPMC 7207 CR2P) of the Palaeontology department of the MNHN. In this thesis, CT-scanning was used for the imaging of large specimens (see Paper V in Annexes). Further CT-scan data will be included in future publications that are currently in preparation.

#### II.2.2.2. SYNCHROTRON LIGHT

The synchrotron radiation is obtained through the acceleration of electrons by spinning in a storage ring (Fig. II.2.2.2.1). An initial electron beam is emitted by an electron gun and accelerated to the speed of light in the linac (linear accelerator). Then, the electron beam is directed to the booster synchrotron, a second circular accelerator that brings the energy levels into operating values. Once the energy reaches these values, the electrons are injected into the storage ring where magnetic devices deflect the trajectory of the electrons. When electrons lose energy they can emit photons, whose properties are selected through a succession of optical instruments, producing the light known as the synchrotron radiation. This light is directed to the experimental stations at the beamlines where it impacts the material. A CCD camera detects and measures the absorbance of the material and produces a series of projections ('slices') that are then processed by a computer (for further information see http://www.esrf.eu).

The major differences in the imaging of the microstructure of fossil specimens between a CT-scan and a synchrotron is that in the latter the power of penetration of the X-ray is increased by many orders of magnitude compared with a CT-scan. The use of phase contrast properties, the flux of photons, and the final voxel size enables to visualize submicron structures in dense samples with a much higher resolution and contrast (TAFFOREAU & SMITH, 2008; SANCHEZ *et al.*, 2012), but also produces 'heavier' data sets. The synchrotron light is thus capable of revealing a great deal of histological features that would be less evident, or even completely hidden in a normal CT-scanning. In the case of scales and fin rays, the imaging power of a CT-scan is often insufficient to observe and properly study the arrangement and microstructure of the different

histological layers. Therefore, the use of synchrotron light has been favoured for those projects where a great level of detail was necessary.

All synchrotron data used in this thesis were imaged at the ID19 beamline of the ESRF, Grenoble, France. Sophie SANCHEZ (UP) performed the synchrotron experiments, with the help of Paul TAFFOREAU (ESRF). Synchrotron light was used in Paper III and further synchrotron data will be included in several publications currently in preparation.

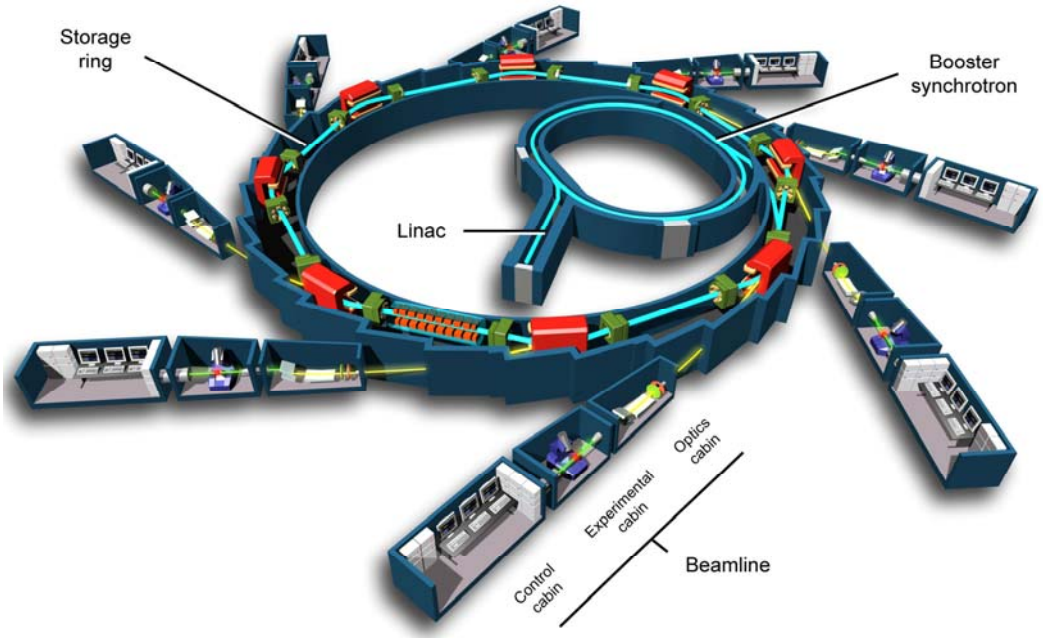



**FIGURE II.2.2.2.1. Schematic representation of a synchrotron.** The outer circular ring (or storage ring) is a particle accelerator that brings electrons (light blue beam) to very high speeds. The electrons are accelerated by electric fields (straight sections between green squares). Magnets bend the beam (red rectangles). When the beam is bent the electrons emit synchrotron radiation (yellow) that is sent into the various beamlines where radiation is processed. Each beamline is divided into an optics cabin where radiation is collected, an experimental cabin where the specimen is deposited, and a control cabin where the data are analysed. © Synchrotron Soleil, modified after their website, www.synchrotron-soleil.fr.

### II.2.3. POST-PROCESSING OF MICROTOMOGRAPHIC IMAGES

After the acquisition of microtomographic images (either via CT-scanning or synchrotron light) begins the long phase post-treatment for getting rid of the acquisition artefacts and three-dimensional virtual reconstruction of the specimens. Segmentation was mainly performed with the software Materialise Mimics ® (v.14.0) (Paper III and VI); Volume Graphics VG Studio Max ® was used for initial observation of large data sets that will be treated in future publications (see Chap V, fig. V.1). All virtual reconstructions were performed in the 'Paleontology Imaging Unit' (UMR CNRS/MNHN/UPMC 7207 CR2P) of the Palaeontology department of the MNHN, Paris.

Each software of microtomographic reconstruction has its particular performances: Mimics® (a medical software) is capable of managing a moderately amount of data and is especially suited to treat CT-scanning images, whereas VG Studio Max® (an industrial software) is reputed by its capacity of handling very large stacks, specially those obtained from synchrotron radiation. Indeed, the resolution of the scans (i.e., the voxel size) determines the number of slices, and this accordingly influences the final size of the stack to be treated. Part of the data treated in this thesis came from synchrotron radiation; however, the use of Mimics® was preferred to VG Studio Max® due to reduced amount of data of interest and the purpose of representation. For instance, for the high-resolution synchrotron data of *Tulerpeton* (Paper III), the image stack was divided in two (PIN 2921/3238 with 5.05 µm of voxel size) or three stacks (PIN 2921/3238 with 0.678 µm of voxel size) in order to treat them separately. After segmentation, data sets from each image stock were joined using Mimics®.

The segmentation principle is similar for both Mimics® and VG Studio Max®, however here I will detail only the principal techniques of segmentation of Mimics®,

since it was my main working software. The Mimics® interface enables to see the stack in all three orientations: axial, sagittal, and coronal (Fig. II.3.2.1). In the treated data, a particular grey-scale threshold had to be defined in order to differentiate the structure of interest from the surrounding matrix. Each threshold defines a coloured mask that corresponds to a given structure (e.g., bone, teeth, osteocyte lacunae, etc.). Masks can be rendered visible, transparent, or invisible in the 3D model by modifying their parameters.

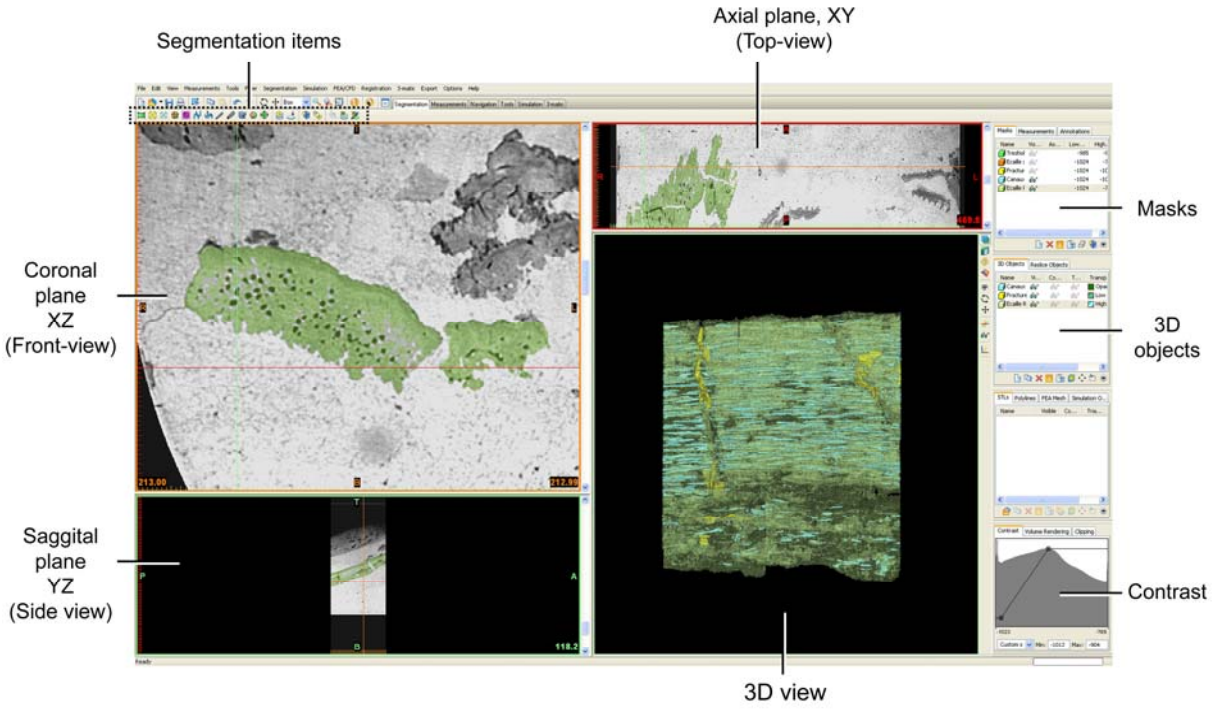



**FIGURE II.2.3.1. Mimics® interface during the treatment of the *Tulerpeton* scales (PIN 2921/3238) images obtained by synchrotron light.** The standard size of each window was modified on purpose to facilitate segmentation (scale margins were more easily seen in the coronal plane) and 3D visualization of the specimen. Masks in the 3D view have been set in transparency to reveal the arrangement of the osteocyte lacunae (in blue) and the path of several major fractures (in yellow).

The structure of interest (e.g., a scale) has to be selected or 'drawn' in every slice where it is present. This step is by far the longest because the selected threshold does not usually fit perfectly to the outer contour of the specimens. In both treatments with Mimics® (Paper III and V), most of the contour delimitation had to be performed manually for each slice (more than hundred images for each project). Each mask is calculated by the software and reconstructed in three dimensions; the resulting virtual reconstruction is then visible in the '3D view' window. Three-dimensional reconstructions of data sets treated separately can be fused to retrieve the complete specimen of interest (see Paper III, Fig.1).

## II.3. EVOLUTIONARY DEVELOPMENTAL BIOLOGY

### II.3.1. HISTORICAL CONTEXT

Evolutionary developmental biology (evo–devo) is the study of how developmental processes evolve to produce new patterns of development, new developmental gene regulation, new morphologies, new life histories and new behavioural capabilities (RAFF, 2000, 2007). Evolutionary developmental biology has its origins in the evolutionary morphology of the late nineteenth century (HALL, 2002). Indeed, developmental biology has always been closely tightened to the study of organism evolution. DARWIN (1859) described differences in animal forms as being the result of natural selection, but he explained their similarities as a result of their shared ancestry. To DARWIN, a close study of embryology would reveal the community of descent between organisms and he encouraged looking to embryonic and larval stages for the recognition of deep homologies that would be obscured in the adult.

DARWIN'S ideas about the importance of embryology in our understanding of the evolution process were developed by his followers. The most famous of them, HAECKEL, established the "biogenetical law" in which phylogeny is the mechanical cause of the ontogeny through the recapitulation mechanism. In HAECKEL's words "ontogeny recapitulates phylogeny" as the organisms development mirrors the main phyletic stages of their evolution.

GOULD (1977) showed that the differences in the interpretation of recapitulation between HAECKEL, who saw ontogeny as the recapitulation of adult forms, and VON BAER, who saw ontogeny as the progressive separation of embryonic forms from a mutual origin, were extremely important. Eventually, developmental data will confirm VON BAER'S laws and discard HAECKEL recapitulation theory.

The four laws of VON BAER can be summarised as follows (after GOULD, 1977):

1. The general features of a large group of animals appear earlier in the embryo than the especial features.
2. Less general characters are developed from the most general, and so forth, until finally the most specialized appear.
3. Each embryo of a given species, instead of passing through the stages of other animals, departs more and more from them.
4. Fundamentally therefore, the embryo of a higher animal is never like the adult of a lower animal, but only like its embryo.

Following VON BAER's principles, GARSTANG (1922) noticed that the evolution of new features was based on changes in developmental stages, not in adult stages. This observation reversed HAECKEL's relationship between ontogeny and phylogeny and GARSTANG remarked that "ontogeny does not recapitulate phylogeny: it creates it."

DE BEER (1954) demonstrated that characters changed their order of appearance in the ontogeny of descendent embryos compared with those of the ancestor, and that some features persist for a greater duration than others. Timing was critical, and any

change in the timing of events could lead to new evolutionary features. For instance, this idea of timing was directly applied by THOROGOOD (1991) in his model of the fin to limb transition. Developmental timing thus became a critical term in all new debates on evolutionary biology.

Despite an enormous amount of developmental data obtained from a large number of species since the end of the nineteenth century, embryology was left out of 'Modern' Evolutionary Synthesis at the middle of the twentieth century. Mainly led by BATESON, who considered that embryology contributed anything to our understanding of the mechanism of evolution, embryology was supplanted by developmental genetics and punctual mutations were viewed as the main "explanatory source" of evolution (GILBERT, 2003b; CARROLL, 2008).

However, GOLDSCHMIDT (1940) and others criticized the mechanism of evolution proposed by the 'Modern Synthesis'. To them, the accumulation of small genetic changes was not sufficient to generate novel macroevolutionary structures. GOLDSCHMIDT claimed that evolution could only occur through inheritable changes in those genes that regulated development, and he presented two models relating gene activity, development, and evolutionary dynamics: 1) the 'developmental macromutations' model, in which new species might originate as 'hopeful monsters' that result from mutations in developmentally important loci; and 2) the 'systemic mutations' model in which chromosomal rearrangements would have the effect of many developmental macromutations and cause even larger phenotypic changes. To GOLDSCHMIDT, the gene was not merely a locus or an allele; it became a 'unit of development'.

WADDINGTON (1953) noted that much variation appeared to be non-genetic and regulated by the environment, and the different rates of evolution seen in the fossil record suggested that the accumulation of small mutations in a local group could not be

responsible for the separation of large lineages. These ideas set the foundations for the theory of 'punctuated equilibrium' stated by GOULD and ELDREDGE (1977).

In his influential book, GOULD (1977) emphasized the importance of heterochrony (i.e., changes in the timing of developmental events leading to changes in morphology) and comparative ontogeny in our understanding of evolutionary processes. The same year, JACOB (1977) proposed his theory of evolution by 'tinkering', in which new biological functions and structures appeared as the result of the use and reshaping of pre-existing components. The discovery of the *Hox* genes in the 80's and the solid establishment of the link between genetics and development (HOLLAND & GARCÍA-FERNÁNDEZ, 1996; BURKE *et al*., 2005; RAFF, 2007) supported JACOB's hypothesis that has successfully integrated evolutionary reasoning nowadays (GILBERT, 2003b).

The current theoretical framework in developmental genetics considers that major anatomical changes are usually the result of mutations affecting the expression of a few genes, especially genes involved in key steps of the embryonic ontogeny (KURATANI, 2009). According to this hypothesis, small differences in the time of activation or in the level of activity of a single gene could in principle considerably influence the systems controlling embryonic development. Despite astonishing similarities of the genotypes between two closely related species, for instance chimpanzees and humans, the phenotypical differences between them would then mainly result from genetic changes in a few regulatory systems. Indeed, much of the current evo–devo research focuses on the evolution of developmental genetic mechanisms (PETTERSON *et al*., 2007).

In-depth analyses of gene interaction and expression enabling evolutionary comparisons between species are well characterized today, but only in model organisms, such as the mouse (*Mus musculus*), the zebrafish (*Danio rerio*), or the fruit fly

(*Drosophila melanogaster*). Unfortunately, these model organisms are sometimes far relatives to the group of study, in our case early tetrapods. However, in recent years new breading techniques have allowed to access developmental data on the Australian lungfish (*Neoceratodus forsteri*), the closest extant sarcopterygian relative to tetrapods (e.g., JOHANSON *et al.*, 2004, 2005a, 2007a,b, 2009; HODGKINSON *et al.*, 2009). These data are beginning to shed light on the genetic and developmental features likely to have been modified during the 'fish-tetrapod transition'.

### II.3.2. THEORETICAL PROTOCOL OF STUDY

As stated above, the universal theoretical framework in evolutionary developmental biology states that any phenotypic difference has its origin in changes in the genetic control of development. However, an important issue in every evo-devo study is the adequacy of interpreting perturbations in precise developmental genes to certain phenotypic modifications.

The standard theoretical protocol of study followed in the developmental biology part of this thesis can be summarised as follows:

- Selection of teratological phenotypes in wild type or mutant fishes as a result of genetic variance (either via mutagenesis or treatment with chemical agents)
- Study of the underlying process of development control of wild type and teratological phenotypes through physiological experiments with inhibitors
- Establishment of a theoretical developmental model accounting for the obtained data
- Adjustment of the morphological and ontogenetic results to the model in order to check predictions
- Proposition of hypotheses about evolutionary processes explaining the fossil morphologies and based on the developmental data

The availability of new powerful tools in developmental genetics (e.g., RT-PCR, *in situ* hybridization, etc.) makes it possible to investigate the roles of genes in development and to define more clearly the mechanisms of development. The experimentation on model organisms enables to tackle a large set of developmental issues and allows focusing on the study of the organs or structures of interest. In the case of this thesis, I used the zebrafish to perform a series of experiments on fin development. The laboratory techniques will be detailed below.

### II.3.3. LABORATORY TECHNIQUES IN DEVELOPMENTAL BIOLOGY

During my stays in the Developmental Biology laboratory of the Málaga University in Spain, I developed my expertise in a diverse set of laboratory techniques for developmental biology studies through a series of experiment on zebrafish embryos. These techniques included the following:

**Care and maintenance of fishes –** Fishes were kept in aquariums at a constant temperature, and were regularly fed. Aquarium water was changed once a week. In order to obtain large numbers of eggs for each experiment, several males and females were kept together in larger tanks. Then, one or two females and a male were put in 'breeding tanks' and fed overnight. A 'breeding tank' consists on a plastic tank containing a steel net placed at the bottom of the tank that separates the swimming adults from the spanning eggs that will sink to the bottom through the small holes in the net. Fertilized eggs were retrieved the next morning. The embryos and larvae were stocked in Petri dishes and placed in an incubator at 28,5$^0$C of temperature for normal development. Water from the Petri dishes was daily changed.

**Inhibitor treatment –** Wild type zebrafish embryos were treated with a genetic inhibitor in order to alter their development and study the role of certain key molecules in fin development. Inhibition of signalling through FGF receptors was performed with the lipophilic reagent SU5402 (MOHAMMADI *et al.*, 1997). SU5402 is a widely used inhibitor of FGF receptor (Fgfr) activation and it is used in a wide range of developmental systems in zebrafish (e.g., POSS *et al.*, 2000; JACKMAN *et al.*, 2004; ABE *et al.*, 2007). SU5402 is useful for assessing requirements for FGF signalling in the late stages of embryonic development because it can be applied in late developmental events such as organogenesis, leaving early FGF-dependent processes unaffected. Embryos were incubated in the dark at 28.5 °C in 1,7 and 0,85 µM SU5402 containing aquarium water, prepared from 5,49 mM SU5402 stock solution in the solvent DMSO. DMSO (0,01%) control embryos were incubated in the dark in aquarium water with the corresponding amount of DMSO. A third fish stock of embryos was incubated in normal conditions as a 'pure' control for comparisons.

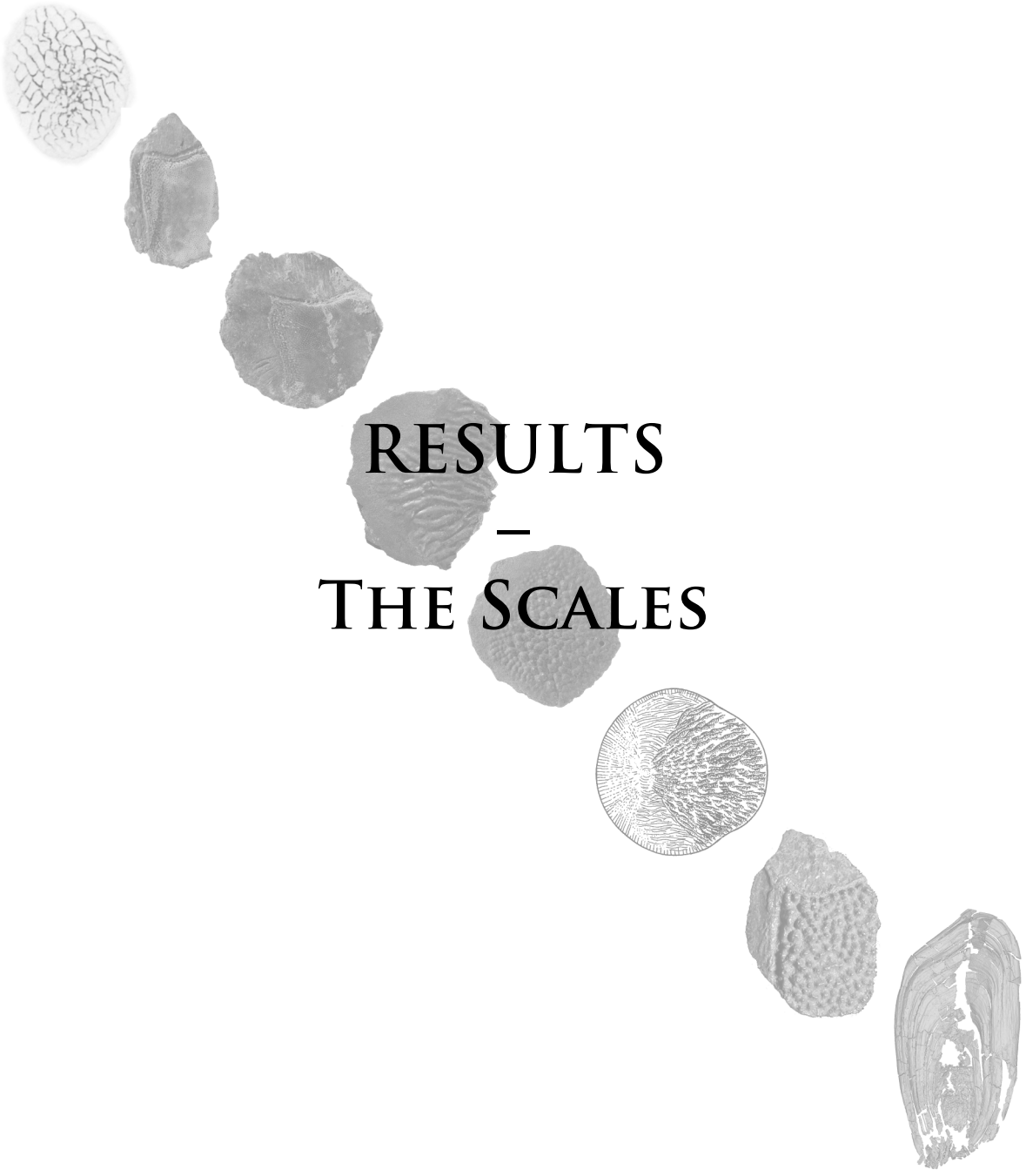
**Heat-shock treatment** – Transgenic zebrafish (bearing a conditional transgene of the dominant negative Fgfr1 that block signalling downstream of all Fgfr subtypes) were breaded as formerly described for the wild type zebrafish. In order to study the role of FGFs in transgenic conditions (as opposed to the inhibitor treatment described above), these mutant fishes were treated with heat-shocks following the protocols described in LEE *et al.* (2005). An electric heater was used for all heat induction experiments. Embryos were placed in six-well plates and placed in the incubator. The six-well plates containing the embryos were then taken out of the incubator and gently placed in the heater. Exposure of one hour in the heater led the embryos to reach 37,5°C. After this, the embryos were returned to incubator temperature (28,5$^0$C).

**Clearing and staining techniques on larval and juvenile specimens** – Clearing and staining techniques are used to observe and study the development of the skeleton in model organisms, such as the zebrafish. After the experimental treatments formerly described (inhibitor treatment and/or heat-shock treatment) the fish larvae were bleached to remove dark pigments from their skin. They were then put in a solution of acetic acid and Alcian blue. Alcian blue is a colorant that primarily dies cartilage through binding with mucopolysaccharides proteins. Muscles are then removed with the use of digestive enzymes (trypsin), allowing the skeleton to be observed more clearly. In order to visualize bone in older larvae, specimens were immersed in an alkaline solution of Alizarin red that binds to calcium of the extracellular matrix in both dermal and endochondral bones. The dyed larvae are then preserved in tubes filled with glycerol and kept in the refrigerator for subsequent observation under a light microscope.

The clearing and staining of the embryos is a very subtle and often frustrating experimental stage. Because of the small size of the specimens, the timing of every step had to be adequate in order to avoid excessive or insufficient dying of the structures of interest. In un-stained larvae, observation under a microscope with Nomarski optics was performed.

**Dissection and photography of the specimens –** Larval specimens preserved in glycerol were transferred to a clean slide in a drop of glycerol in order to perform dissections and photograph them. For instance, for the study of the pectoral fin development, the postcranial region was removed and a sagittal section of the head was performed with a razor blade under a dissecting microscope. Caudal fins were observed in complete specimens. Embryos were placed in a slide with two small coverslips spaced from each other in order to create a small central compartment. The whole system was

then covered with a large coverslip, avoiding the crushing of the embryo, but gently pushing the coverslip down until the embryo was held in place. Slides were then observed under a Nikon Microphot microscope with a mounted Nikon camera.



# RESULTS
# –
# THE SCALES

BEMIS, 1984
Paper I
JARVIK, 1980
Paper III

# I. GENERAL INTRODUCTION

> […] *it is true that the application of cut and dried definitions of the scaling will no longer enable us satisfactorily to subdivide the Pisces into Placoidei, Ganoidei, Cycloidei, and Ctenoidei;* [and] *it is true that "placoid" scales may be present in the Ganoidei, and that various forms of cycloid scales may have been independently evolved from rhomboid ganoid scales in later groups, nevertheless these facts do not by any means prove that the scaling is of little systematic importance.*
>
> GOODRICH, 1904

As put forward by GOODRICH more than hundred years ago in his two influentil papers (1904, 1907), the study of scale morphology and histology has become a somewhat undervalued field of palaeontology. Indeed, scales have been generally neglected as a strong phylogenetic feature of osteichthyan interrelationships due to their inherent convergent properties. Moreover, the extreme abundance of scale remains in certain fossil sites, sometimes belonging to a single taxon, has turned the scales into a rather 'banal' material of study. Nevertheless histological structures may play a new and important role in heated phylogenetic debates and a good knowledge of scale morphology can be revealed as extremely valuable in the study of faunal associations in fossil sites. New recent studies (e.g., ZYLBERBERG *et al.*, 2010; FRIEDMAN & BRAZEAU, 2010; CHEN *et al.*, 2012) have upgraded the status of scales as a more informative feature than previously thought, in the study of phylogenetic reconstruction, character evolution, and morphofunctional implications.

This chapter comprises three studies dealing with the morphological and histological evolution of the scales of two main groups of sarcopterygians: porolepiforms (Paper I and II) and tetrapods (Paper III).

**I** **Mondéjar-Fernández J.** & Clément, G. 2012. Squamation and scale microstructure evolution in the Porolepiformes (Sarcopterygii, Dipnomorpha) based on *Heimenia ensis* from the Devonian of Spitsbergen. *Journal of Vertebrate Paleontology*, 32(2): 267-284.

**II** **Mondéjar-Fernández J.** & Janvier, P. *Submitted*. A holoptychiid porolepiform (Sarcopterygii, Dipnomorpha) from the Frasnian of Colombia, with remarks on the Late Devonian Euramerica-Gondwana vertebrate faunal interchange. Ready for submission to the *Journal of South American Earth Sciences*.

**III** **Mondéjar-Fernández, J.**, Clément, G., Lebedev, O. & Sanchez, S. The scales of *Tulerpeton curtum* and the Devonian origin of the tetrapod squamation Bauplan. Ready for submission to *PNAS*.

In Paper I, I wrote the article, completing the former description of the material by Gaël CLÉMENT, and produced all figures (except the reconstruction in fig. 11 drawn by Sophie FERNANDEZ in the MNHN). In Paper II, I wrote the majority of the article and produced all the figures. In Paper III, I wrote the article and produced all figures (excepting the SEM pictures of fig.1 performed by Oleg LEBEDEV in the PIN). In all Papers I shared the interpretation and discussion of the results with the other co-authors.

## SQUAMATION AND SCALE MICROSTRUCTURE EVOLUTION IN THE POROLEPIFORMES (SARCOPTERYGII, DIPNOMORPHA) BASED ON *HEIMENIA ENSIS* FROM THE DEVONIAN OF SPITSBERGEN

The porolepiform *Heimenia ensis* from the Early-Middle Devonian of Spitsbergen was first published by ØRVIG (1969b) based solely on isolated scale material. Since its initial description, ØRVIG became puzzled by the fact that two very different scale morphotypes, i.e, rhombic and rounded, could be attributed to a single sarcopterygian taxon (Fig. I.1,2), moreover that both morphotypes were characteristic of the two defined families of Porolepiformes: the Porolepididae with rhombic scales, and the Holoptychiidae with rounded scales.

When I began searching for material for this thesis, I became very interested in the case of *Heimenia*. My supervisor Gaël CLÉMENT had already worked on its cranial anatomy (CLÉMENT, 2001a) and had discussed its peculiar squamation in his PhD (CLÉMENT, 2001b). He was in possession of an exquisite and unpublished specimen of a nearly complete body of *Heimenia* where the entire squamation was preserved. Moreover, numerous acid-prepared isolated scales attributed to *Heimenia* that were also at my disposal in the collections of the MNHN.

In order to better understand all aspects of the transition from a rhombic to a rounded scale morphotype in the porolepiforms I focused on the morphology and distribution of the scales in the body specimen and perform a series of palaeohistological cross sections on the abundant isolated scale material. The combination of anatomical and histological observations allowed me to discuss the differences between morphotypes and the recognition of evolutionary trends in the scales of porolepiforms.

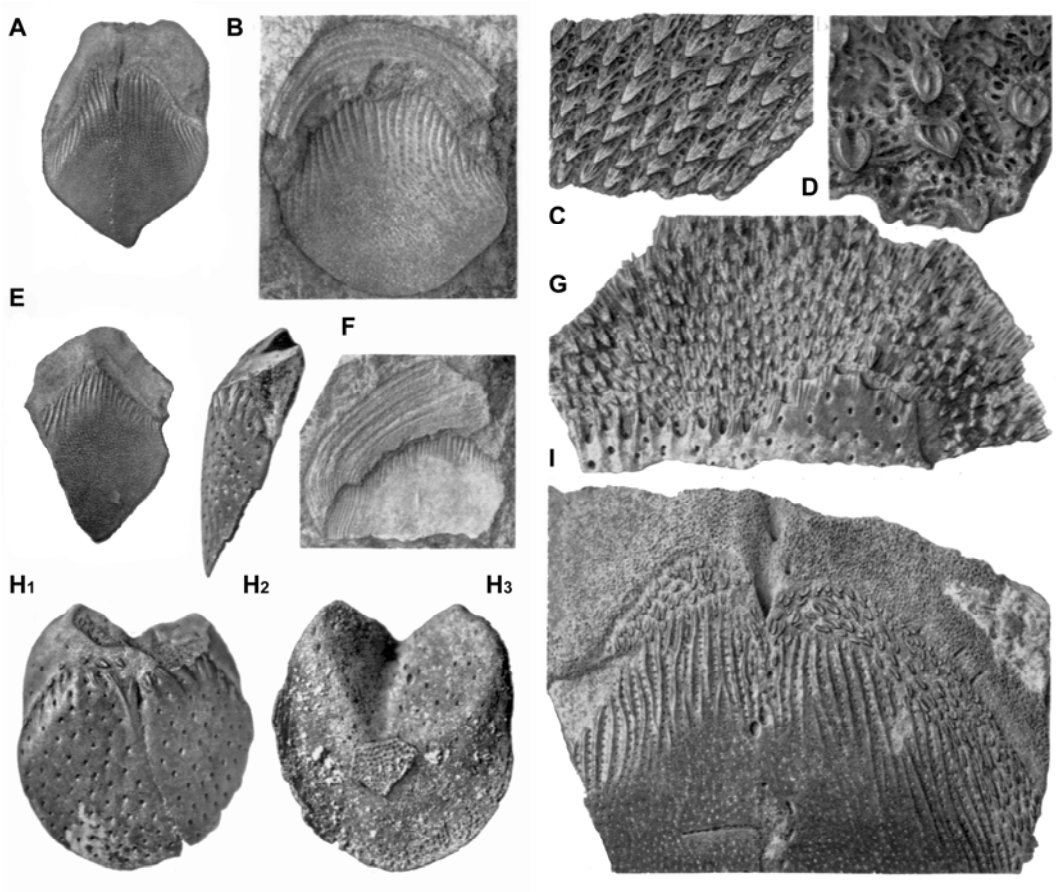



**FIGURE I. 1. *Heimenia ensis*, scales from the Verdalen valley, Andree Land, Vestspitsbergen** (upper Early or lower Middle Devonian). **A.** Lateral line scale, SMNH P 6476; X 9/4. **B.** Holotype, rounded scale showing impressions of cosmine and some peripheral bone annulae on the internal surface, SMNH P 6475; X 9/4. **C.** Fragment of rounded scales showing radiating rows of small dentine tubercles (odontodes), SMNH P 6478; X 22.5. **D.** Fragment showing larger dentine tubercles, SMNH P 64 79; X 22.5. **E.** Fragment of a similar scale as the holotype, BMNH P 49759; X 9/4. **F.** Incomplete rhombic scale, PMO A 32743; X 9/4. **G.** Another fragment of rounded scale showing both radiating rows of small odontodes (as in C) and a cosmine layer with anterior ridges (as the scales in A,E), SMNH P 6480; approx. X 11. **H.** Small, somewhat incomplete scale, probably occupying a position at the base of one of the fins, shown in superficial (**H1**), basal (**H2**) and lateral view (**H3**), SMNH P 6477; X 15. **I.** Detail of the anterior part of a lateral line scale showing lateral line pores and a pit-line, the anterior ridges on the cosmine, and the zone of free odontodes just anteriorly to the cosmine, BMNH P 49760; X 7,5. Modified after original figs. 5,6 in ØRVIG, 1969b.

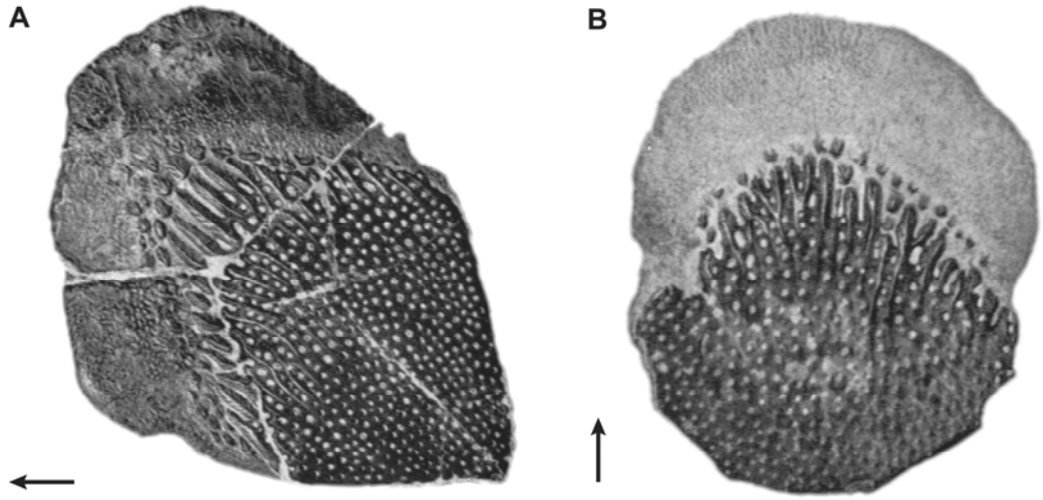



**FIGURE I.2. *Heimenia* sp., scales from the Anderson River, District of Mackenzie, Northwestern Canada**, Upper Lower or Lower Middle Devonian. The scales come from a dark shale that also yielded remains of *Melanognathus* and *Dialipina*. **A.** Rhombic scale, NMC- 11621; X 5; reversed from original. **B.** Rounded scale, NMC-11620; X5. Modified after original fig. 7 in ØRVIG, 1969b. Arrows point anteriorly.

Based on my observations of the body specimen of *Heimenia* I identified three scale morphotypes: rhombic, rounded, and intermediate (the latter being somewhat subjective and corresponding to scales located midway of the trunk). The transition from one scale morphotype to the other appears to be progressive. The palaeohistological study also confirmed this point since no abrupt differences were observed between morphotypes, only slight changes in thickness and arrangement of the different histological layers.

In *Heimenia*, a continuous cosmine covering is present in all scale morphotypes, even in the rounded-most scales. The presence of cosmine in rounded scales is a rather uncommon condition in sarcopterygians but it is present in certain Devonian dipnoans (e.g., *Dipterus*, *Griphognathus*) (e.g., SCHULTZE, 1969a), although not as continuously developed as in *Heimenia*. Therefore it has been generally considered that cosmine

cannot be found in rounded scales, a condition probably related to developmental or morphofunctional constraints of the cosmine that very often restrict its presence to the rhombic morphotype.

The phylogenetic position of *Heimenia* is currently not fully resolved since no precise phylogenetic analysis of porolepiform interrelationships has been published since the work of SCHULTZE (2000), who did not include *Heimenia* among the surveyed taxa. CLÉMENT (2001b) placed *Heimenia* in a trichotomy with *Porolepis* and the clade Holoptychiidae, thus turning the Porolepididae into a possible paraphyletic assemblage of primitive porolepiforms. *Heimenia* possess several features that are primitive for the porolepiforms (CLÉMENT, 2001b) but shows other that approach the holoptychiid condition, especially those concerning the squamation. Therefore, Clément (2001b) suggested that *Heimenia* would constitute a transitional form between *Porolepis* and the holoptychiids, although cladistics analyses did not confirm it.

The scales of "porolepidids" such as *Porolepis* and *Heimenia* are morphologically very close to the primitive condition of the rhombic, cosmine-covered scales of early sarcopterygians from the Early-Middle Devonian, such as *Youngolepis* (LU & ZHU, 2008). On the other hand, the scales of holoptychiids, devoid of cosmine and ornamented with dentine ridges and/or tubercles are very similar to those of actinistians, and could be easily mistaken (JOHANSON & RITCHIE, 2000).

The break-up of the cosmine in porolepiforms was not directly studied in my Paper I on *Heimenia*. Several holoptychiid scales loan form the MB of Berlin were sectioned and observed for comparisons; preliminary discussions on this issue will be detailed below (see Discussion). The loss of a continuous cosmine covering and its replacement by an array of tubercles and ridges occurred in porolepiforms in parallel with other groups of sarcopterygians (e.g., "osteolepiforms") that also show primitive

members with rhombic and cosmine-covered scales (e.g., "osteolepidids", megalichthyids) and derived forms with rounded, cosmine-less scales (e.g., *Canowindra*, tristichopterids).

Since the body specimen was preserved in 3D, it was probable that the internal postcranial skeleton was also preserved below the squamation. A series of CT-scans performed in the AST-RX platform of the MNHN in Paris were carried out a few months ago, but unfortunately the rocky matrix appear to be too dense for our CT-scan and no clear structures could be observed, nor modelled. In the future, the use of more powerful techniques of imaging, like the synchrotron light, would certainly enable to get working images of the inside of this specimen and broaden our knowledge on the axial skeleton of porolepiforms, which is currently known solely from *Glyptolepis* from the Late Devonian of Scotland (ANDREWS & WESTOLL, 1970b; AHLBERG, 1991).

Finally, my first approach on the squamation of a Devonian sarcopterygian enabled me to familiarise with palaeohistological techniques and histological descriptions. It laid the foundations for further palaeohistological studies on scales (see Paper III) and confronted me with major evolutionary issues concerning the squamation of fishes.

# Paper I

Journal of Vertebrate Paleontology 32(2):267–284, March 2012


ARTICLE

# SQUAMATION AND SCALE MICROSTRUCTURE EVOLUTION IN THE POROLEPIFORMES (SARCOPTERYGII, DIPNOMORPHA) BASED ON *HEIMENIA ENSIS* FROM THE DEVONIAN OF SPITSBERGEN

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ABSTRACT—New material of the "porolepidid" *Heimenia ensis* (Porolepiformes, Dipnomorpha, Sarcopterygii), sheds light on the evolution of scale morphology in sarcopterygian fishes. This material consists of an articulated, nearly complete body and numerous isolated scales from the Emsian-Eifelian (upper Lower Devonian) of Spitsbergen. *Heimenia* squamation can be described as 'transitional' between that of *Porolepis* and the more derived Holoptychiidae. The cosmoid scales of *Heimenia* are divided into three morphotypes: (1) rhombic, (2) intermediate, and (3) rounded. The rounded scales are present in the anterior third of the trunk, intermediate scales occupy its middle third, and rhombic scales extend in the rear and all over the ventral region. The transition between scale morphotypes is progressive along the body. All scales bear traces of a cosmine covering, regardless of their overall shape. Paleohistological study shows that the relative thickness of the cosmine layer decreases whereas the relative thickness of the bony basal layer increases from the rhombic to rounded scales. This unique squamation provides new information about the evolutionary transition from thick/rhombic scales covered with cosmine to thin/rounded scales lacking cosmine in the Porolepiformes. Such morphological and histological changes also occurred by convergence among different groups of Middle–Late Devonian sarcopterygians (e.g., lungfishes and "osteolepiforms"). In *Heimenia*, the presence of rounded scales in the anterior part of the body is here regarded as an adaptation to a dynamic and agile life style and constitutes a new example to support the hypothesis of the anteroposterior spread of derived characters in fishes.

## INTRODUCTION

The Porolepiformes are an exclusively Devonian group of lobe-finned fishes (Sarcopterygii) that inhabited near-shore environments from the early Lochkovian (earliest Devonian) to the late Famennian (latest Devonian). The taxon was erected by Berg (1937) on the basis of *Porolepis*. Jarvik (1942) gathered the families Porolepididae (comprising *Porolepis* and *Heimenia*) and Holoptychiidae (comprising *Holoptychius*, *Glyptolepis*, and *Laccognathus*, among others) in the order Porolepiformes. The monophyly of the group has been well established (Cloutier and Ahlberg, 1996), although some questions remain concerning the possible paraphyly of the "Porolepididae." The Porolepiformes are currently considered as the sister group of lungfishes, forming together the Dipnomorpha (Ahlberg, 1991) (Fig. 1).

The Porolepiformes are characterized by the presence of dendrodont-type teeth (Schultze, 1969; Panchen and Smithson, 1987), sub-squamosal bones (Cloutier, 1990; Ahlberg, 1991; Cloutier and Schultze, 1996), absence of (differentiated) intertemporal and supratemporal bones, contribution of the nasal series to the skull roof margin posterior to the orbit (Ahlberg, 1992a), and by the otic part of the main lateral line canal passing through the radiation center of the postparietal bones (Ahlberg, 1991). The Porolepiformes are neither taxonomically nor morphologically diverse, and little is known about their skeletal morphology or phylogenetic relationships. Outgroup comparison shows that the characters defining the "Porolepididae" are plesiomorphic for the Porolepiformes. The "porolepidids" differ from the holoptychiids in having a longer anterior cranial division and a posteriorly shallow lower jaw, and a cosmine covering on the scales and dermal bones (Ahlberg, 1992b), but beside those characters there is little morphological variation between both families.

The evolutionary history of the Porolepiformes during the Devonian was marked by the transition from a squamation composed of thick and rhombic scales covered with cosmine in the "porolepidids", to thin and rounded scales lacking cosmine in the more derived holoptychiids. These characters used to be considered as mutually exclusive and characteristic of the two families within the Porolepiformes.

Cosmine is a derived feature for sarcopterygians (Friedman and Brazeau, 2010). It can be defined as an association of hard tissues composed of vascular bone, dentine, and enamel. The enamel forms a shiny, superficial layer overlying the dentine. The dentine contains a characteristic and complex pore-canal network, which opens to the surface through pores in the enamel (Goodrich, 1907; Ørvig, 1969a; Sire et al., 2009). The oldest known example of a cosmine-like pore-canal system comes from the stem sarcopterygian *Meemannia eos*, from the early Devonian of China (Zhu et al., 2006). Cosmine has also been reported in other early sarcopterygians, such as *Psarolepis*, *Achoania*, and *Styloichthys* (Yu, 1998; Zhu et al., 1999; Zhu and Ahlberg, 2001; Zhu and Yu, 2002). The putative stem sarcopterygian *Guiyu oneiros* from the Ludlow of China (Zhu et al., 2009; Quiao and Zhu, 2010) does not seem to possess cosmine.

Cosmine is widespread in fossil sarcopterygians, but unknown in living forms. Nevertheless, only some of the Devonian Sarcopterygii possessed cosmine; it is not present in all porolepiforms, lungfishes, "osteolepiforms", and it is absent from stem tetrapods. Previous studies considered that coelacanths and onychodontids lacked cosmine (Meinke, 1984). However, new discoveries and phylogenetic interpretations have shown that cosmine was present in the putative most basal fossil coelacanth

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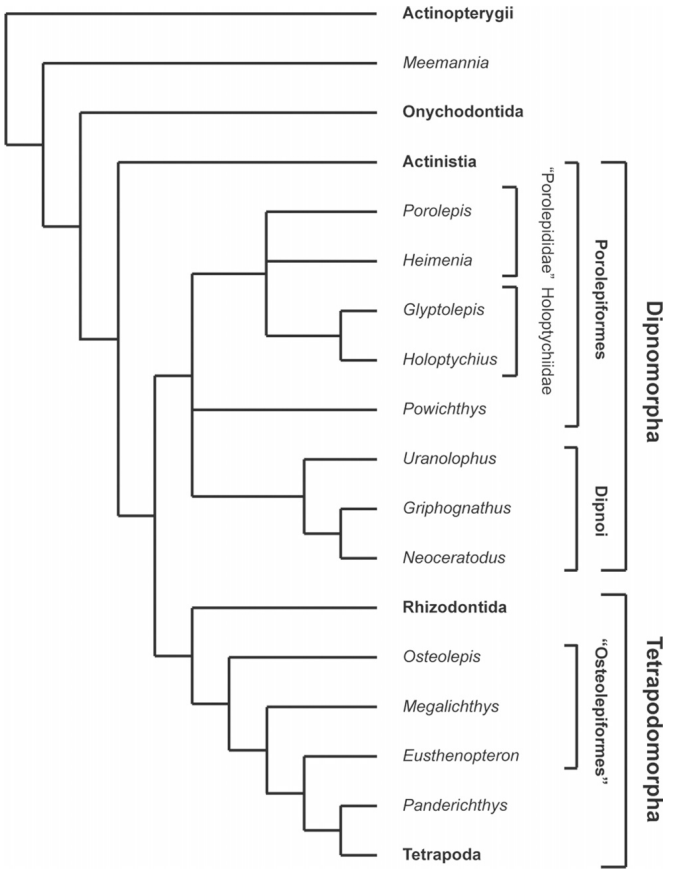


FIGURE 1. Simplified cladogram of consensual sarcopterygian phylogenetic relationships with special reference to the Porolepiformes including various taxa discussed in the main text (after Clément, 2001b).

*Styloichthys* (Friedman, 2007) and the earliest onychodontids (Zhu and Zhao, 2005; Lu and Zhu, 2010). In these early forms (such as *Meemannia*), a pore-canal network is not associated with a single enamel-dentine layer but rather with superimposed enamel-dentine couplets (Friedman and Brazeau, 2010; Zhu et al., 2010). Among more crownward sarcopterygians, 'true' cosmine (sensu Sire et al., 2009), bearing a single layer of enamel overlying dentine tubercles that are resorbed altogether prior to the deposition of a new layer, is present in rhipidistians (sensu Cloutier and Ahlberg, 1996; Janvier, 1996) comprising the Dipnomorpha and the Tetrapodomorpha. Cosmine characterizes cosmoid scales (Francillon-Vieillot et al., 1990), yet its function is not clearly known. According to Thomson (1975), it could have had housed electrosensory organs but Borgen (1989, 1992) and Bemis and Northcutt (1992) suggested that it could have been a vascular complex involved in the deposition and resorption of mineralized tissues. Cosmine is one of the few morphological and histological vertebrate structures that have no homologue among extant forms (Ørvig, 1969a).

*Heimenia* was first described by Ørvig (1969b) on the basis of isolated scales from the Upper Emsian of Spitsbergen. A lower jaw later described by Jarvik (1972:pl. 12:6) was also assigned to *Heimenia*. *Heimenia* occurs in the Emsian and Eifelian of Vestspitsbergen (Verdalen Member of the Stjørdalen division, Wood Bay Formation) (Ørvig, 1969b). The genus currently comprises a single species: *Heimenia ensis* Ørvig, 1969. The type specimen of *H. ensis* is a scale (Ørvig, 1969b:fig. 5B) from the Verdalen Member of the Stjørdalen division (Lower to Middle Devonian) of Spitsbergen. Other fragmentary *Heimenia*-like scales are also known from northwestern Canada (Anderson River, District of Mackenzie; Jarvik, 1967; Schultze, 1968; Ørvig, 1969b), Poland (Holy Cross Mountains; Ørvig, 1969b; first described as "*Porolepis* ex grege *posnaniensis*" by Kulczycki in 1960), the Baltic Region (Lyarskaya, 1981), possibly from the Belarusian and Lithuanian sites of Kupceli, Tauragé, and Viduklé (Clément, 2001a), Germany (Klerf Beds of the Eifel, Rhineland Massif; Jessen, 1989), Vietnam (Bacbun Formation, Trang Xa; Thanh and Janvier, 1987), and China (Haikou Formation, Ludian, Yunnan; Wang, 1986).

Here we describe for the first time a well-preserved, nearly complete body of *Heimenia ensis* from Spitsbergen. The exceptional preservation of the in situ scale rows and of some isolated scales offers the opportunity to study in detail the squamation pattern and the scale microstructure of this "porolepidid". The evolutionary and morphofunctional implications of this unique squamation will be discussed.

**Institutional Abbreviations**—**LIG**, Institute of Geology and Geography, Vilnius, Lithuania; **MNHN**, Muséum National d'Histoire Naturelle, Paris, France.

## SYSTEMATIC PALEONTOLOGY

Class OSTEICHTHYES Huxley, 1880
Subclass SARCOPTERYGII Romer, 1955
Order DIPNOMORPHA Ahlberg, 1991
Suborder POROLEPIFORMES Berg, 1937

*HEIMENIA ENSIS* Ørvig, 1969b
(Figs. 3–9)

## MATERIALS AND METHODS

### Material

The *Heimenia* material described herein is in deposit in the Bâtiment de Paléontologie, MNHN, Paris. It was collected in 1986 by Dr. Valentina Karatajute-Talimaa (Vilnius, Lithuania) in the Verdalen Member of the east coast of Andree Land (Gjelsvikfjellet, Skamdalen) in the island of Spitsbergen (Svalbard archipelago, Norway) (Fig. 2). The Verdalen Member was regarded to be early Eifelian by Ørvig (1969b) but Emsian in age by Blieck et al. (1987). More recently, Mark-Kurik (1991) considered the Stjørdalen division and its lateral equivalent, the Verdalen Member (upper part of the Wood Bay Formation), as lower Emsian in age, because of its correlation to the *dehiscens* to *inversus-laticostatus* conodont zone(s).

The *Heimenia* material consists of scattered endocranial and dermal elements (previously described by Clément, 2001a) found in association with isolated scales. The fossil remains were recovered from a 2 m long and 0.5 m thick lens composed of black limestone located within layers of dark clay of the Grey Hoek Formation (Fig. 2B). The "porolepidid" scale remains were associated with odontode-like scales of the thelodont *Amaltheolepis* sp., scales of the acanthodian *Ptychodyction* sp., and dermal plates of the euleptaspid placoderm *Herasmius granulatus*.

There is no doubt that the isolated scales belong to the same genus, and most probably the same species defined by Ørvig (1969b) as *Heimenia ensis*. A few isolated scales have well-preserved dentine tubercles on the leading edge of the cosmine and numerous altered scales show concentric growth zones. The diagnostic characters of these scales, the striking morphological similarity to those described by Ørvig (1969b), their abundance in the sediment and, especially, the fact that no other sarcopterygian remains have been found in a lens of this formation, allow assigning this new "porolepidid" material to the species *Heimenia ensis*.

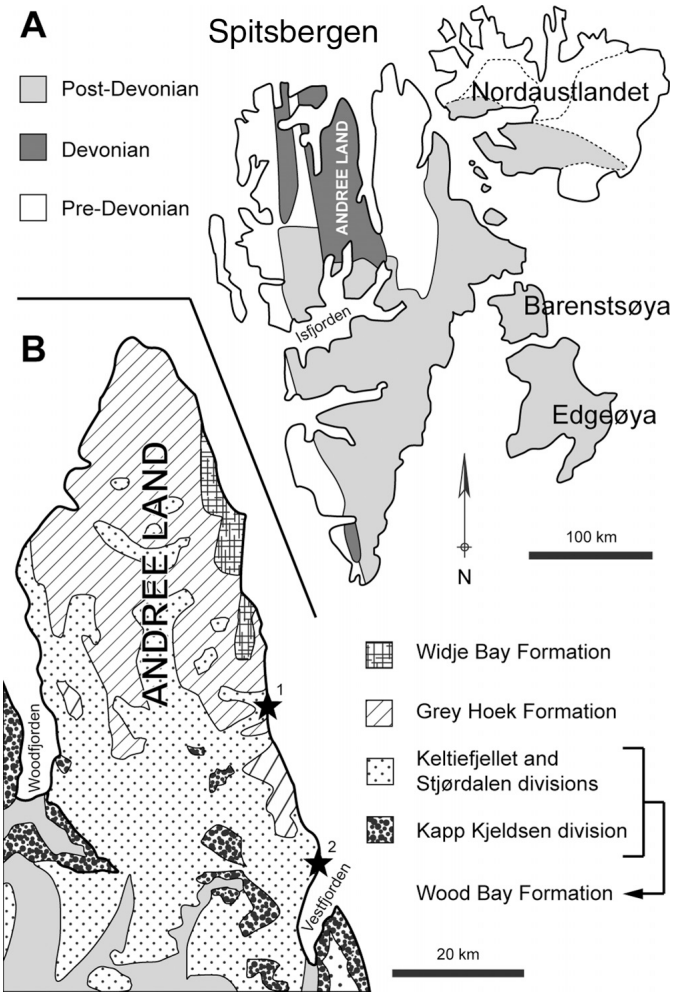


FIGURE 2. **A**, Schematic geological map of the Svalbard archipelago and the island of Spitsbergen (after Goujet, 1984). **B**, geological map of the Devonian deposits of the Andree Land peninsula of the Spitsbergen island (after Blieck et al., 1987). Stars indicate fossil localities: **1**, *Heimenia* isolated scales; and **2**, *Heimenia* nearly complete body.

An almost complete headless and finless articulated body of *Heimenia* (LIG 45-2027) collected by Dr. Yuri P. Burov (St. Petersburg, Russia) in the west coast of Vestfjorden (Keltiefjellet and Stjørdalen divisions) is also comprised among this new material (Fig. 2B). The specimen is preserved in three dimensions. The entire specimen is 310 mm long, its greatest height is 130 mm, and its average thickness is 45 mm (Figs. 3, 4). The individual probably had a lower body height in his lifetime, the fossil specimen being flattened laterally.

The surface of the body is slightly weathered. The shape and arrangement of the scales are clearly visible but the cosmine covering has been lost during fossilization in some areas, although some scales, especially in the ventral region, still bear traces of cosmine. The good preservation of the squamation makes this specimen extremely interesting, because it shows a progressive morphological transition from rhombic to rounded scales.

The specimen is broken into two pieces; the crack is located anteriorly to the basal plates of the second dorsal and anal fins (Figs. 3, 5). The bases of the pectoral, pelvic, and first dorsal fins are visible in the large piece (Fig. 3), whereas the bases of the anal and second dorsal fins are visible in the smallest piece (Fig. 5). The base of the caudal peduncle forms the posterior end of the specimen.

The specimen is identified as a "porolepidid" because the cleithrum presents the characteristic porolepiform shape (Jarvik, 1972), and several slightly altered associated scales show a cosmine covering. This specimen can certainly be referred to the genus *Heimenia*, because the squamation is composed of numerous characteristic rounded scales associated with many rhombic scales. These characters correspond to the diagnosis of the species *Heimenia ensis* established by Ørvig (1969b) (based exclusively on isolated scale morphology). Moreover, this specimen comes from the top of the Keltiefjellet and Stjørdalen divisions, in which isolated *Heimenia* scales have already been found (Ørvig, 1969b).

## Methods

More than a hundred isolated scales were prepared using a 10% dilution of formic acid. Only about 50 of them are complete or nearly complete. Different scale morpholotypes were prepared. The scales were embedded in stratyl resin and sectioned for their histological study with a thickness of approximately 25–30 $\mu$m. The ground sections were examined under natural transmitted and polarized light with a Zeiss Axiovert35.

# RESULTS

## Body Squamation

In specimen LIG 45–2027 (Figs. 3–5), the entire squamation of the body is preserved, except at the base of the median fins and at the posterior-most tip of the caudal peduncle. In the large piece (Fig. 3), there are approximatively 28 scale rows along the lateral line, ranging from the row located dorsally to the cleithrum (Fig. 4) to the row anterior to the posterior fracture. The rows are slightly oblique and anteromedially oriented. The number of scales per row is between 20 and 22 from the dorsal to the ventral median scale row. The anterior border of the first dorsal fin (Fig. 4) appears to be located at the level of the 25th scale row. The anterior border of the pelvic fin basal plate (Fig. 4) is located at the level of the 18th scale row and the posterior end of the anal fin basal plate (Fig. 5) is located at the level of the 24th scale row. In the small piece (Fig. 5), there are 10 scale rows that follow those of the larger piece (Figs. 3, 4), making a total count of 38 preserved scale rows. The anterior border of the basal plate of the second dorsal fin (Fig. 5) is located at the level of the 34th scale row, its rear end being located at the level of the 37th scale row.

According to their general external shape, the cosmoid scales can be divided into three different morphological types: (1) rhombic, (2) intermediate, and (3) rounded (the term cycloid or circular scales will not be used in this study to avoid confusion with the cycloid scales of the teleosts, which possess a different histological structure). The rounded scales are present in the anterior third of the body, intermediate scales are located in the middle third of the trunk, and rhombic scales are present in its posterior third. Small rhombic scales are also present all over the ventral region. The largest rounded scales are located in the anterodorsal region, behind the extrascapular bones and the dorsal part of the cleithrum. The transition from rhombic to rounded scales is progressive along the body. Below the level of the ventral-most margin of the paired fins the scales of the ventral region are rhombic in overall shape, and smaller than any other scales of the squamation. Cosmine remnants are more visible in these scales than in any other region of the body, probably due to a better preservation related either to a thicker cosmine layer in the scales of the ventral region or a lesser exposure of the ventral surface.

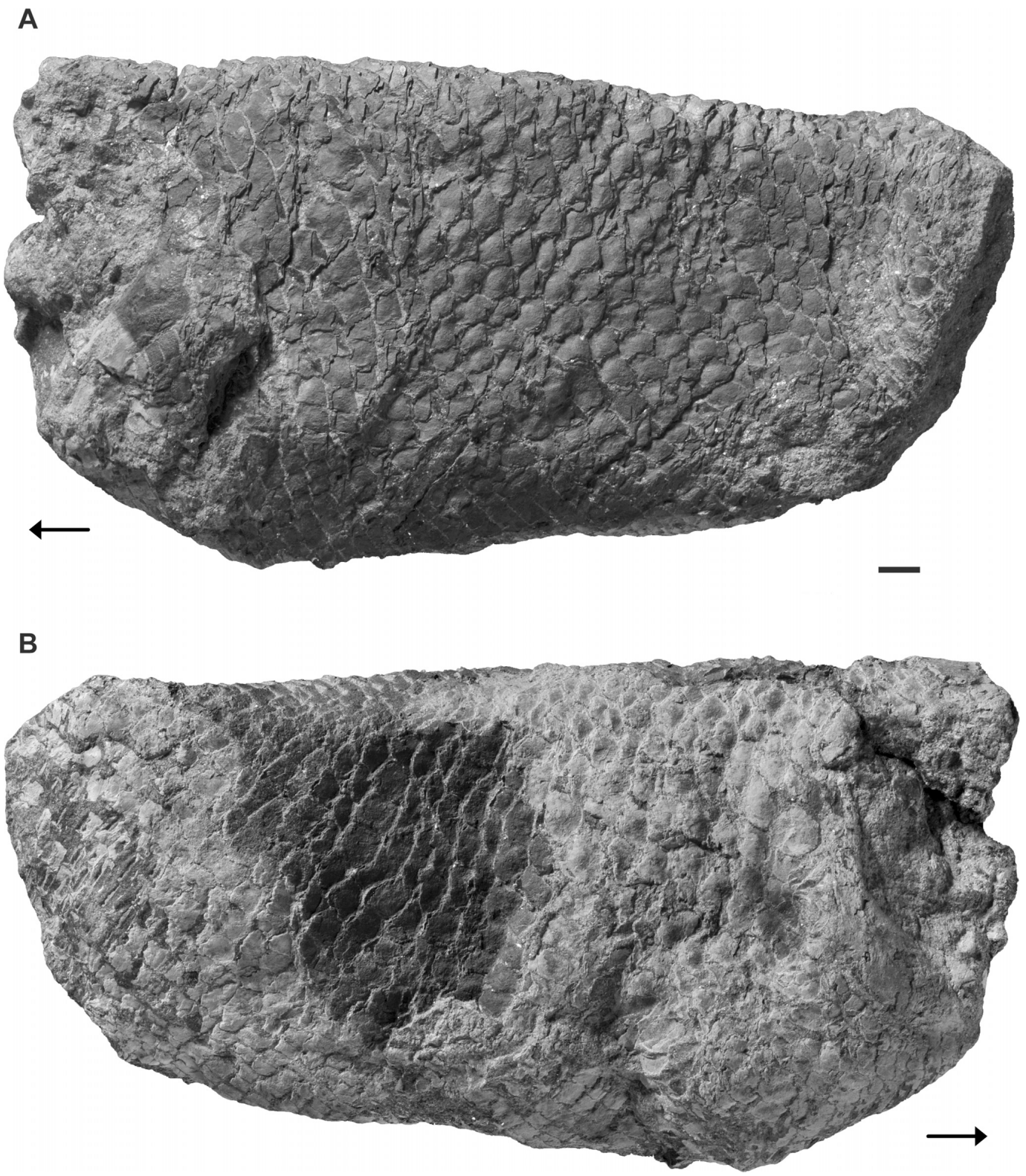


FIGURE 3. *Heimenia ensis* Ørvig, 1969b, LIG 45–2027. **A**, left lateral side of the specimen without the posterior fragment. **B**, right lateral side of the specimen. Arrow points anteriorly. Scale bar equals 1 cm.

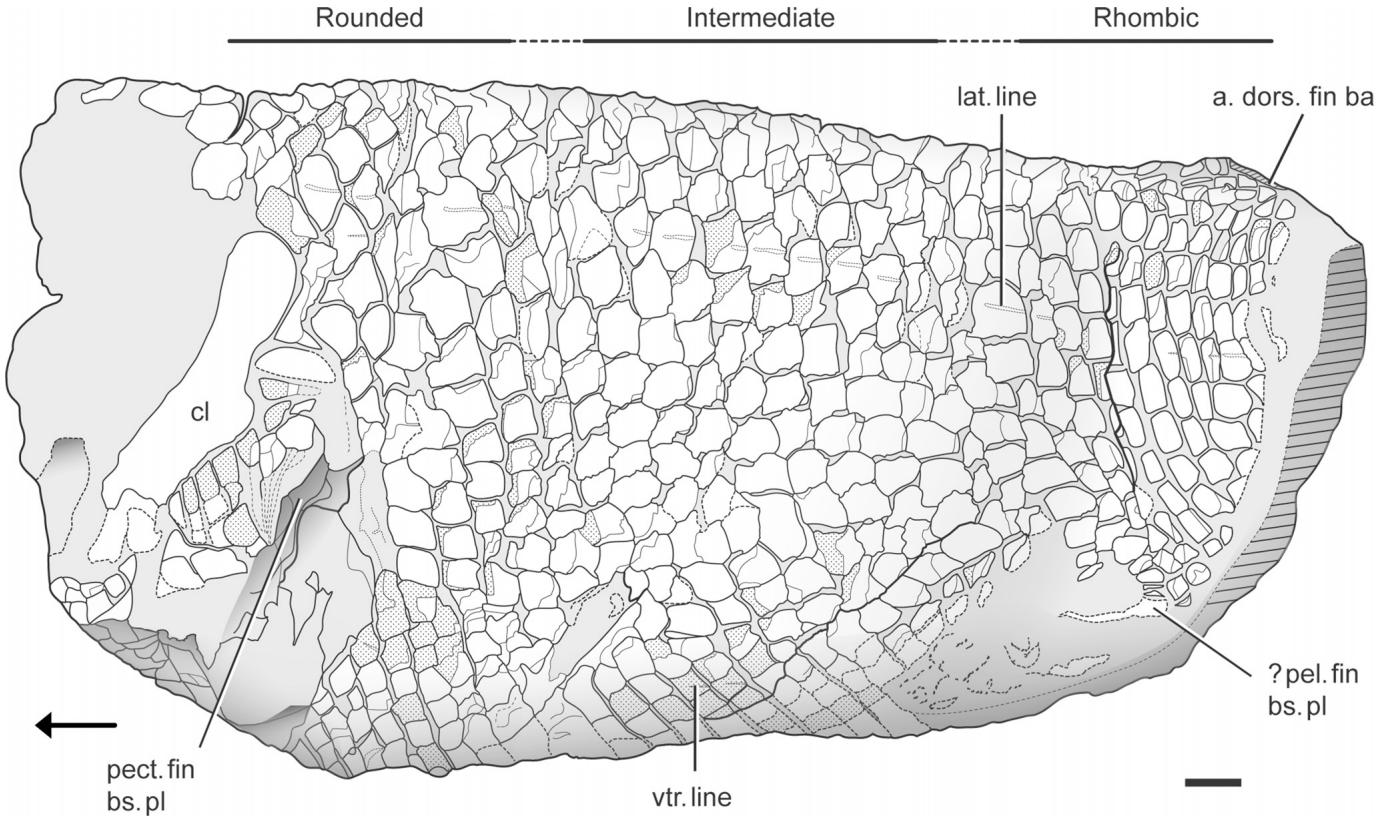


FIGURE 4. *Heimenia ensis* Ørvig, 1969b, LIG 45–2027, interpretative illustration of the left lateral side of the specimen. Notice the progressive transition from rhombic, to intermediate, to rounded scale morphotype. **Abbreviations**: **a. dors. fin ba**, anterior dorsal fin base; **cl**, cleithrum; **lat. line**, lateral line; **pect. fin bs. pl**, pectoral fin basal plate; **?pel. fin bs. pl**, pelvic fin basal plate; **vtr. line**, ventral line. Arrow points anteriorly. Scale bar equals 1 cm.

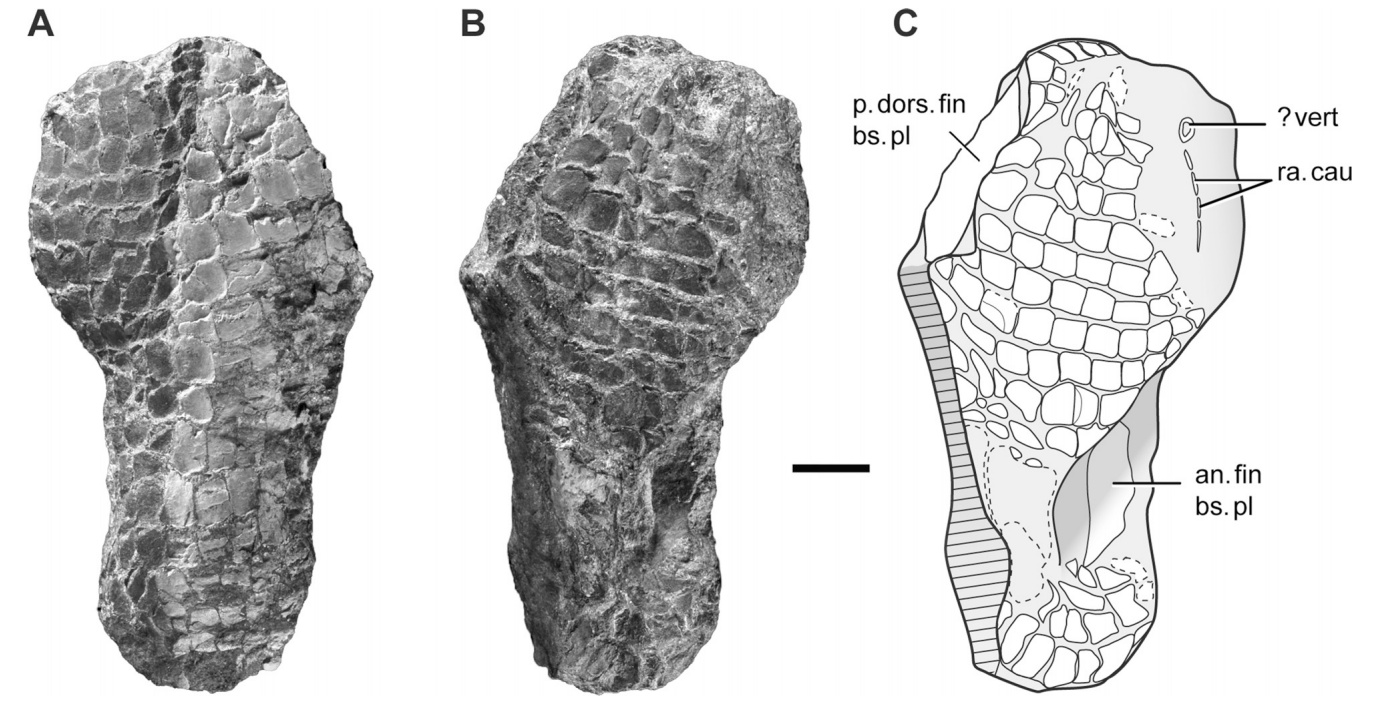


FIGURE 5. *Heimenia ensis* Ørvig, 1969b, LIG 45–2027, posterior fragment of the specimen. **A**, right lateral side; **B**, left lateral side; **C**, interpretative drawing of the left lateral side. **Abbreviations**: **an. fin bs. pl**, anal fin basal plate; **p. dors. fin bs. pl**, posterior dorsal fin basal plate**; ra. cau**, caudal radials; **?vert**, vertebrae. Scale bar equals 1 cm.

The free exposed surface of each scale is rectangular in the rhombic scales of the posterior part of the body, diamond-shaped in the intermediate scales of the middle part, and semicircular in the rounded scales of the most anterior part of the body (Figs. 3, 4). The scales are arranged in a slate-like way, in which each scale is overlapped dorsally by the scale of the same oblique row and overlapped anteriorly by the adjoining scale.

In the dorsal part of the specimen, a dorsal median row of scales is visible. Due to the flattening of the specimen, this dorsal scale row can be more easily seen in the dorsal anterior third of the trunk. The scales are rounded to hexagonal in shape and some of them bear traces of a cosmine covering. The anterior facet is overlapped by the posterior portion of the anteriorly neighboring scale of the median row. In the ventral region, a ventral median row of scales is also visible, although not as clearly as the dorsal one. Ventral median scales are only visible in the anterior and posterior third of the specimen. The scales are rhombic to square in shape and run along the ventral margin of the specimen.

The path of the lateral sensory line (Fig. 4) is observed in the dorsal half of both flanks and extends from the back of the skull to the caudal peduncle (Figs. 3, 4). In some of the ventral scales, a row of pits indicates part of the path of the left ventral sensory line (Fig. 4).

### Isolated Scales

*Heimenia* scales vary greatly in size, ranging from 14 to 36 mm in length (from the dorsal to the ventral margin of the scale) and from 12 to 25 mm in width; the smallest being the rhombic ones and the largest, the rounded ones. The scales are fairly thin, especially the rounded ones, with an average thickness ranging from 1 to 3 mm (Fig. 6).

**External Surface**—The external surface of the scales is divided in two different areas: a smooth, anterodorsal overlapped area and a sculptured median exposed area (Fig. 6A1–F1). The exposed area of all the isolated scales available for study shows a cosmine covering. Even if the scales have a rounded outline, the cosmine covering shows, in almost all cases, a more or less rhombic-like or diamond shape. The overlapped areas of the rounded scales and certain intermediate scales are extremely large and tend to become thin on their margins. They join in their anterodorsal part forming a semicircular outline of the anterodorsal margin of the scale.

Several rhombic scales (Fig. 6D1) show the characteristic 'peg' in their anterodorsal portion. Such peg is also present in the scales of *Porolepis* (Gross, 1966) and is considered to be a primitive character for osteichthyans (Friedman and Brazeau, 2010). The peg disappears in the intermediate and rounded scales due to the expansion of the anterodorsal overlapping surfaces, giving to the anterior part of the scales a more rounded outline (Fig. 6B1, C1, E1, F1).

The rounded shape of certain scales is due to a pronounced expansion of the anterior and dorsal overlapping surfaces, and accentuated by a tendency to convexity on the ventral and posterior margins of the scales. A digitation of the dorsal margin of the dorsal overlapped area is visible in certain rounded and intermediate scales (Fig. 6C1, E1), a condition similar to that of *Powichthys thorsteinssoni* (Jessen, 1975, 1980). No trace of an anteroventral process, particularly developed in *Powichthys spitsbergensis* and sometimes present in other basal sarcopterygians (Clément and Janvier, 2004), seems to occur in *Heimenia*, although some scales show a slight anteroventral expansion of the anterior overlapped area (Fig. 6B1). A groove separating the overlapped areas from the cosmine-covered exposed portion is visible in all scale types, especially in the rhombic scales, as in *Porolepis* (Ørvig, 1957) and the "osteolepidids" (Ørvig, 1957; Jarvik, 1980), although it is less marked in the intermediate and rounded scales. This groove is usually better defined at the base of the dorsal overlapped area than at the base of the anterior overlapped area of the scales.

The anterior and dorsal margins of the cosmine covering of the *Heimenia* scales show a characteristic elongated ridge system. The ridges are usually more abundant in the anterior margin of the cosmine. Between the ridges, the cosmine pores are arranged in rows. The cosmine pores are slightly elongated anteroposteriorly and are bordered anteriorly by a slight crescentiform elevation (Jarvik, 1980; Janvier, 1996), therefore their anterior border is slightly more elevated than the posterior one. The pores are usually large (0.1 to 0.25 mm in diameter), showing a diameter increase towards the cosmine margins. The anterior margin of the cosmine shows tiny isolated tubercles that are variable in number. The posterior-most tubercles are covered by an enamel layer. These tubercles are slightly concave on their upper face and show a characteristic spoon or horseshoe-like shape (Ørvig, 1969b). The overlapped area of the scales is not ornamented.

**Internal Surface**—The internal surface of the scales is either flat or slightly concave. The rhombic scales normally show a broad and elongated elevation (keel or articular ridge) on their internal surface (Fig. 6A2). The keel divides the internal surface of the scales into two slightly unequally sized areas: a large anterior area and a small posterior one. This articular ridge is less evident in some intermediate scales or completely absent in several large rounded scales (Fig. 6B2, C2, E2, F2).

A ventrally located concave area is associated with the articular ridge in the internal surface of the scales. This area, triangular to round in shape, corresponds to the 'socket,' the overlapping area associated with the 'peg' of the adjoining ventral scale. In the rhombic scales, the socket is narrow and deep, and it is located ventromedially in the inner face of the scales directly contacting the ventral margin of the keel (Fig. 6A2). In the intermediate and rounded scales, the overlapping area is larger and occupies the anteroventral quarter of the inner face of the scale (Fig. 6B2, C2, E2, F2). In the more rounded scales, the socket disappears, leaving only a slight rounded depression in the anteroventral part of the inner face of the scale (Fig. 6C2, F2). At the periphery, the internal surface of a few rounded scales shows rings of bone growth (the "terraced bone annulae" described by Ørvig, 1969b:286). This annular growth is also known in the scales of the holoptychiids, where the growth rings are, however, more visible.

**Lateral Line Scales**—The lateral sensory line scales found among the new *Heimenia* material are similar to those described by Ørvig (1969b:fig. 6D). They are flat to slightly convex, a usual condition in holoptychiids but very different from that of *Ventalepis* (Schultze, 1980:fig. 1), where the scales are strongly vaulted. The anterior foramen (Fig. 7) of the lateral line is located in the external surface, in the anterodorsal apex of the cosmine covering. The posterior foramen (Fig. 7) is located in the internal surface near the posterior rim of the scale. The foramina are about 1 mm in diameter (Fig. 7). In their external exposed area, the smallest sensory line scales show an anteroposterior alignment of pores larger than those of the pore-canal system of the cosmine. The biggest scales, rounded in shape, also show an alignment of pores (Fig. 7) located posterior to the anterior foramen and a set of large pores randomly located in the central region of the scale (Fig. 7A).

**Remarks**—A small scale unlike any other was described by Ørvig (1969b: fig.5E). This scale is comparatively thick and the anterior part of its internal surface shows a high 'V'-shaped concavity. Its exposed external surface is nearly circular in shape with short ridges in the anterior region of the cosmine and very few dentine tubercles anterior to the cosmine. Ørvig (1969b) considered that this isolated scale was certainly located at the base of a fin. A scale with a similar shape has been identified above the basis of the left pectoral fin (Fig. 4) in the nearly complete body specimen (Figs. 3, 4). This scale has a heart shape and shows an anteroposteriorly oriented elevation that expands in the pos-

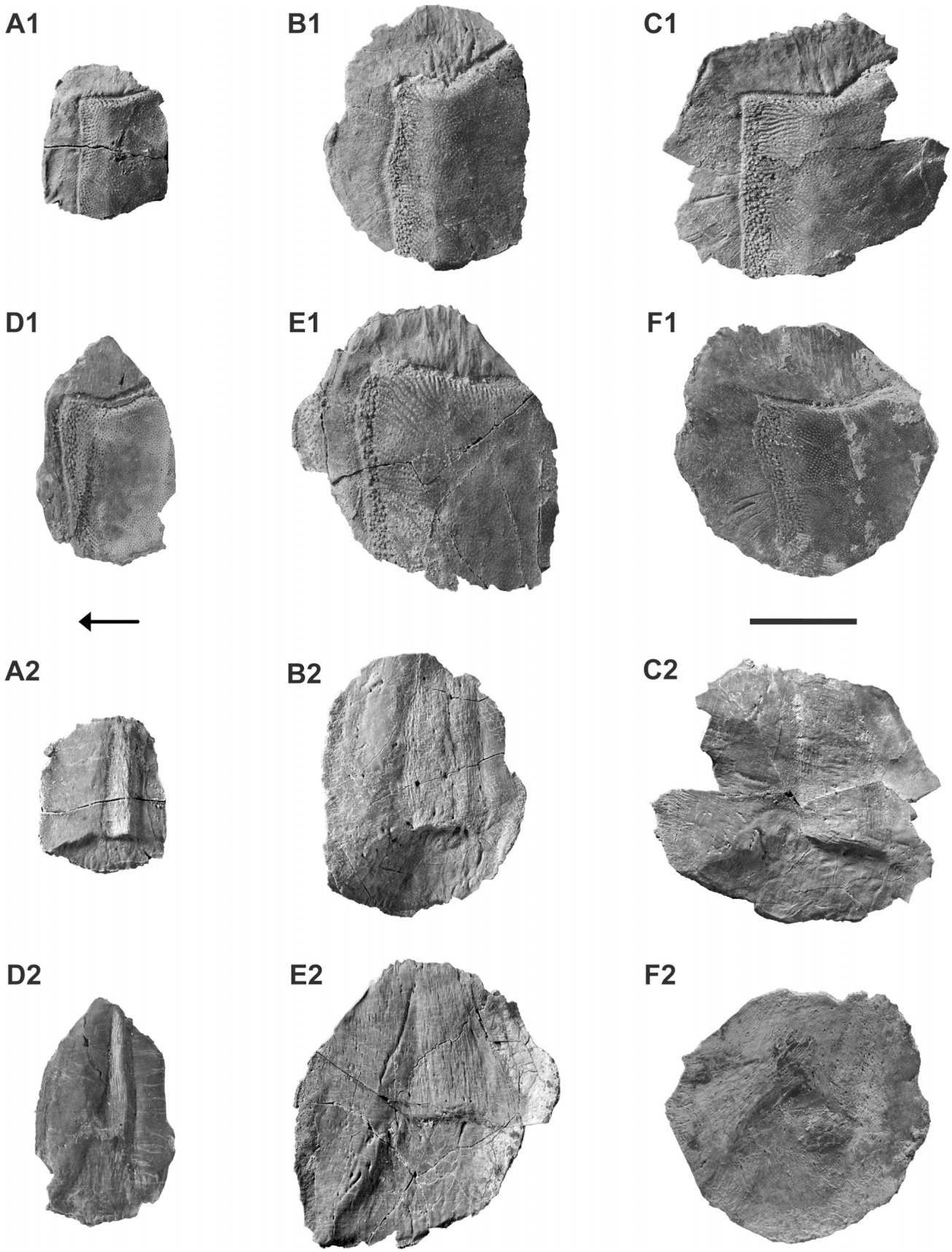


FIGURE 6. *Heimenia ensis* Ørvig, 1969b, isolated scales. **A1**–**F1**, external view; **A2**–**F2**, internal view. **A**, **D**, rhombic morphotype (**A**, LIG 45–2042; **D**, LIG 45–2030); **B**, **E**, intermediate morphotype (**B**, LIG 45–2045; **E**, LIG 45–2049); **C**, **F**, rounded morphotype (**C**, LIG 45–2050; **F**, LIG 45–2018). Arrow points anteriorly for the scales in external view. Scale bar equals 1 cm.

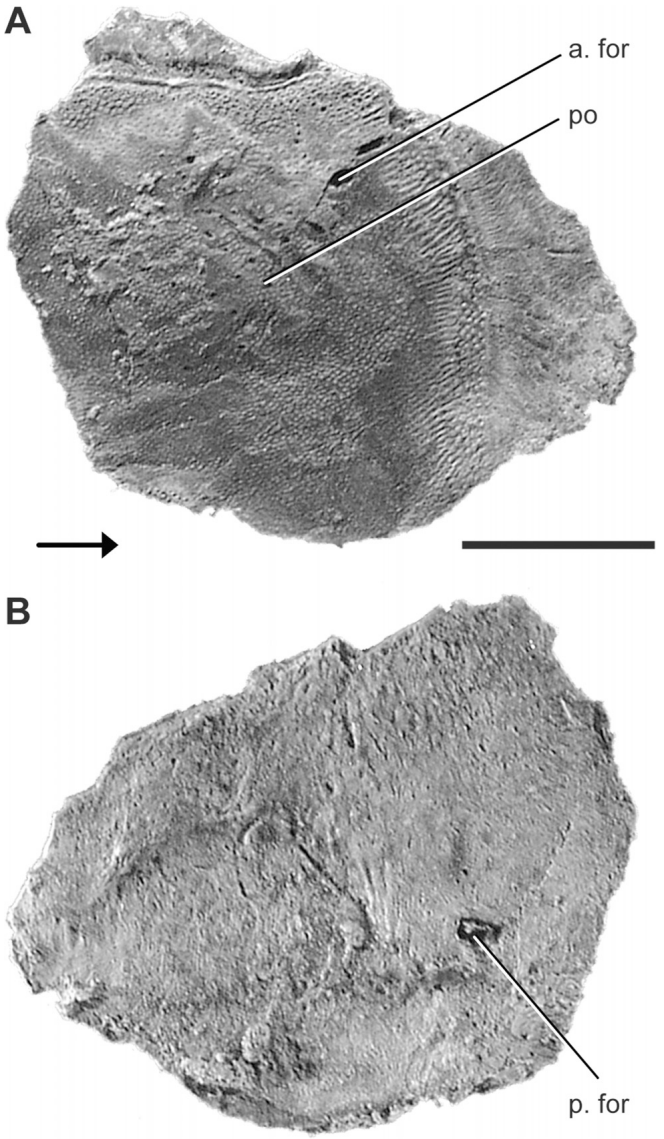


FIGURE 7. *Heimenia ensis* Ørvig, 1969b, isolated right flank lateral line scale (LIG 45–2037). **A**, external view (arrow points anteriorly); **B**, internal view. **Abbreviations**: **a. for**, anterior foramen; **p. for**, posterior foramen; **po**, pore. Scale bar equals 1 cm.

teroventral region. The enamel covering in this region is shinier than in other parts of the scale. Although the internal surface cannot be seen, the elevation of the median part could be easily correlated with the 'V'-shaped inner concavity of the scale figured by Ørvig (1969b). Thus it seems that Ørvig's assumption concerning the location on the squamation of this isolated scale was correct.

### Scale Histology

The *Heimenia* scales can be described as typical cosmoid scales (see Gross, 1956; Francillon-Vieillot et al., 1990). The classical cosmoid scale is composed of four different layers, from top to bottom: (1) enamel (or enameloid), (2) dentine, (3) middle vascular bone, and (4) basal lamellar bone. The overlapped areas of the scales are solely composed of vascular and lamellar bones (Fig. 8). This structure is homogenous in all *Heimenia* scales, regardless of their overall shape (Fig. 8).

**Enamel**—The enamel layer is thin and constitutes a single layer. The absence of cellular processes spreading from the underlying dentine layer confirms the presence of enamel, and not enameloid, in *Heimenia*. The enamel does not penetrate in the cosmine pores, although it can form a slight bulge on the margins of the canals (Fig. 9A1, B1, C1). The thickness of the enamel layer is constant throughout the scale surface for each scale morphotype, with an average thickness of 15 $\mu$m.

**Dentine**—The dentine of *Heimenia*, as in the other Porolepiformes scales, can be described as orthodentine (Ørvig, 1967, 1977; Francillon-Vieillot et al., 1990; Sire et al., 2009). The dentine shows pulp cavities, from which radiate dentine tubules (cytoplasmic processes of the odontoblasts) almost perpendicular to the overlying enamel layer. The dentine layer contains the horizontal and vertical canals forming the characteristic cosmine pore-canal system (Porenkanalsystem of Gross, 1956) (Fig. 9A1, B1, C1). There is no evidence for underlying odontodes below the dentine layer, as in *Porolepis* or *Glyptolepis* (Gross, 1956). The thickness of the dentine layer varies from one scale type to the other. In the rhombic scales, the dentine has an average thickness of 150 $\mu$m, whereas in the intermediate and rounded scales, its thickness is between 250 $\mu$m (intermediate) and 300 $\mu$m (rounded).

**Middle Vascular Layer**—Between the dentine and the basal lamellar bone layers lies a densely vascularized middle layer, composed of woven-fibered cellular bone. Some vascular canals connect the middle vascular layer with the dentine canals (Fig. 8). There is no trace of resorption lines in this vascularized middle layer for any studied scale.

In the rhombic scales, the middle layer is well developed and densely vascularized, appearing thus as cancellous, especially in the central region of the scale. Its thickness increases in the center of the scales and decreases towards the margins, ranging from 300 $\mu$m in the anterior and posterior margins to 900 $\mu$m in the central region.

In the intermediate scales, the middle layer is also densely vascularized, especially in the central region, and appears to be more cancellous than in the rhombic and rounded scales. Its thickness variation throughout the scale shows a pattern similar to that of the rhombic scales. The thickness of the middle vascular layer ranges from 700 $\mu$m in the anterior margin of the cosmine to 1500 $\mu$m in the central region, at the level of the internal keel.

In the rounded scales, the middle vascular layer is less cancellous than in the rhombic and intermediate scales. The thickness of the vascular bony layer is globally constant throughout the scale, ranging from 400 $\mu$m in the anterior region to 700 $\mu$m in the center and to 300 $\mu$m in the posterior part of the scale.

**Basal Layer**—Located under the middle vascular layer lies a basal layer composed of lamellar cellular bone that is globally uniform and well developed in all the different scale morphotypes (Fig. 8). The collagen fibers lie parallel to each other and are closely packed together, arranged in plies in a plywood-like structure (see Meunier and Géraudie, 1980; Meunier, 1984), thus corresponding to the original definition of isopedine (Pander, 1856; Meunier, 1987). There are about 7–15 collagen plies, depending on the thickness of the basal lamellar layer. Each ply is composed of numerous collagen fibrils oriented in the same direction. Several osteocyte lacunae and primary and secondary vascular canals (or osteones) are visible between the collagen plies (Fig. 9A2–3, B2–3, C2–3). The walls of the secondary osteones are separated from the surrounding bone by cementing lines, thus attesting of resorption processes at this level (Fig. 9B3). Sharpey's fibers occur, passing across the basal layer (Fig. 9B2); their direction is approximately perpendicular to the scale surface.

In the rhombic scales, the collagen plies seem to be arranged orthogonally, their orientation changing of approximately 90° between the plies. However, this pattern is not constant throughout the scale (Figs. 8, 9A2–3). The isopedine layer is thin when

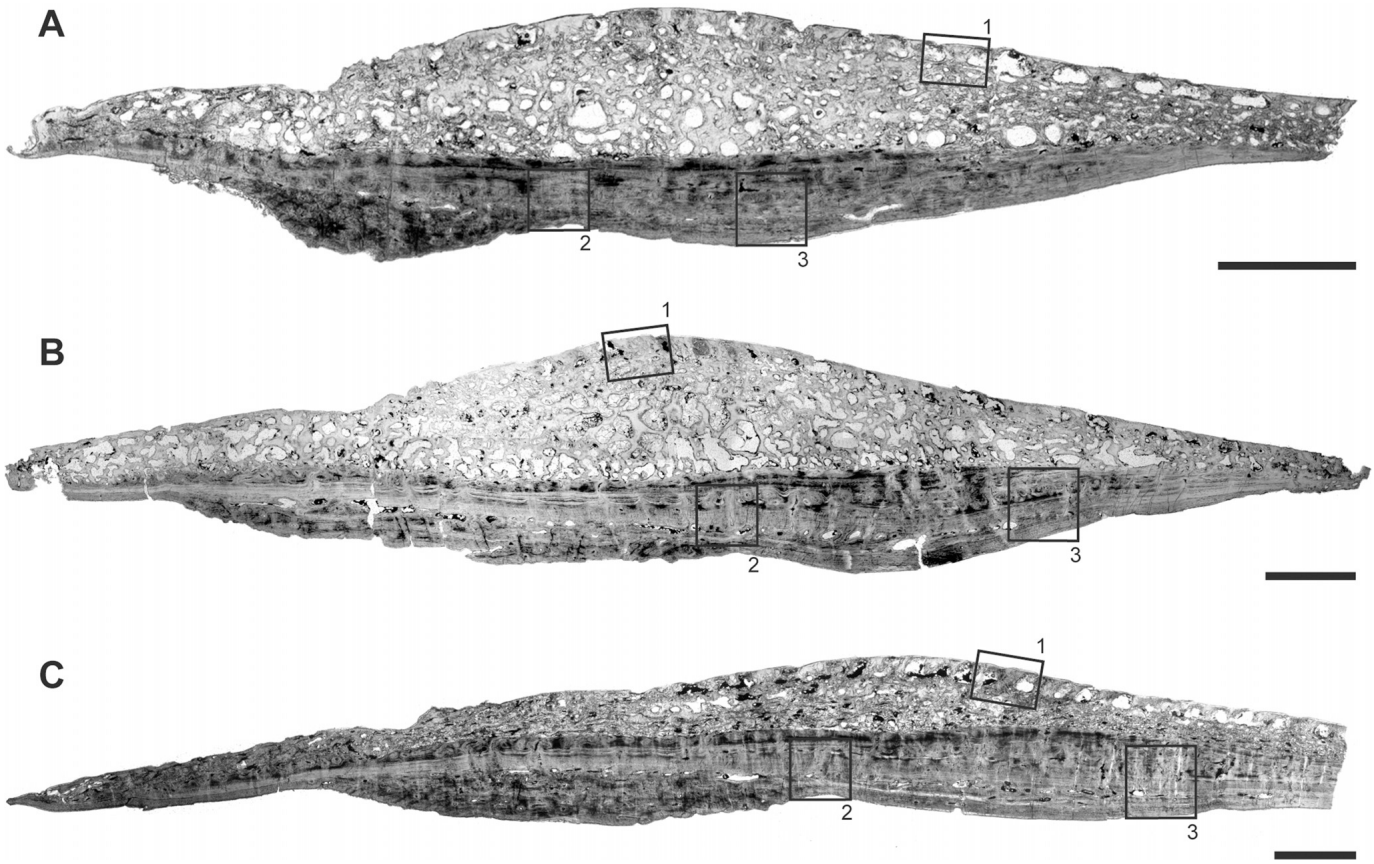


FIGURE 8. Vertical ground sections of *Heimenia ensis* Ørvig, 1969b, isolated scales. **A**, LIG 45–2042 (rhombic morphotype); **B**, LIG 45–2045 (intermediate morphotype); **C**, LIG 45–2050 (rounded morphotype). The insets are detailed in higher magnification in Figure 9. Scale bars equal 1 mm.

compared to the vascular bone middle layer and shows a constant average thickness of 300 $\mu$m, constituting about 1/3 of the scale total thickness (Fig. 8A).

In the intermediate scales, the orientation of the collagen plies varies relatively to the more or less orthogonal arrangement seen in the rhombic scales, the collagen plies being twisted throughout the scale; however, in certain regions the collagen plies could still show an orthogonal arrangement (Fig. 9B2–3). The isopedine layer is thicker and more vascularized than in the rhombic scales. The thickness of the isopedine layer is generally constant throughout the scale, with an average thickness of 600 $\mu$m. The ratio between the vascular bone layer and the basal lamellar bone layer exceeds 33% but does not reach 50% (Fig. 8B).

In the rounded scales, the collagen plies are no longer orthogonally arranged and show a more continuous twisted arrangement along the scale than in the intermediate scales (Fig. 9C2–3). The thickness of the isopedine layer is more or less constant throughout the scale, showing a slight thickness increase from the central to the posterior region. Its thickness ranges from 300 $\mu$m in the anterior region, to 500 $\mu$m in the center, to 800 $\mu$m in the rear. The ratio between the vascular bone layer and the basal lamellar bone layer reaches 50% (Fig. 8C).

**Internal Bone Tissue**—In the middle part of most of the scales, and below the isopedine layer, lies a bony zone that constitutes the internal articular ridge, or keel, of the typical rhomboid scale (sensu Francillon-Vieillot et al., 1990). Sharpey's fibers are present in the keel (Fig. 8); their direction is approximately perpendicular to the scale surface as in the basal bony layer. In the rhombic scales, the keel is well developed, but restricted to the anterior region, with a maximal thickness of 450 $\mu$m (Fig. 8A). In the intermediate scales, the keel is less developed than in the rhombic scales, but it is still present; the bony area being more elongated, spreading over the internal surface of the scale (Fig. 8B). Its maximal thickness is 450 $\mu$m. In the rounded scales, the articular ridge has disappeared externally; however, the internal bone tissue forming the keel is still visible in the anteromedial part of some scales, although not as clearly developed as in the intermediate and rhombic scales. Its maximal thickness is 700 $\mu$m (Fig. 8C).

## DISCUSSION

The scales of *Heimenia* correspond very well to what could be called an 'intermediate' morphological stage in the evolutionary transition from rhombic to rounded scales in the Porolepiformes. The morphological characteristics of the *Heimenia* scales fall between those of *Porolepis* and the holoptychiids. *Porolepis* shows a squamation composed of rhombic scales only (except for some large specimens in which large scales tend to present a 'rounded' shape in the anterodorsal region of the body). On the other hand, the holoptychiids show a squamation composed exclusively of rounded scales. Both scale character states (primitive and derived) can be found in our new *Heimenia* material. Concerning the ornamentation variation, some scales show two states of character simultaneously: a primitive one known in "porolepidids" (e.g., a cosmine covering ornamented with ridges in its

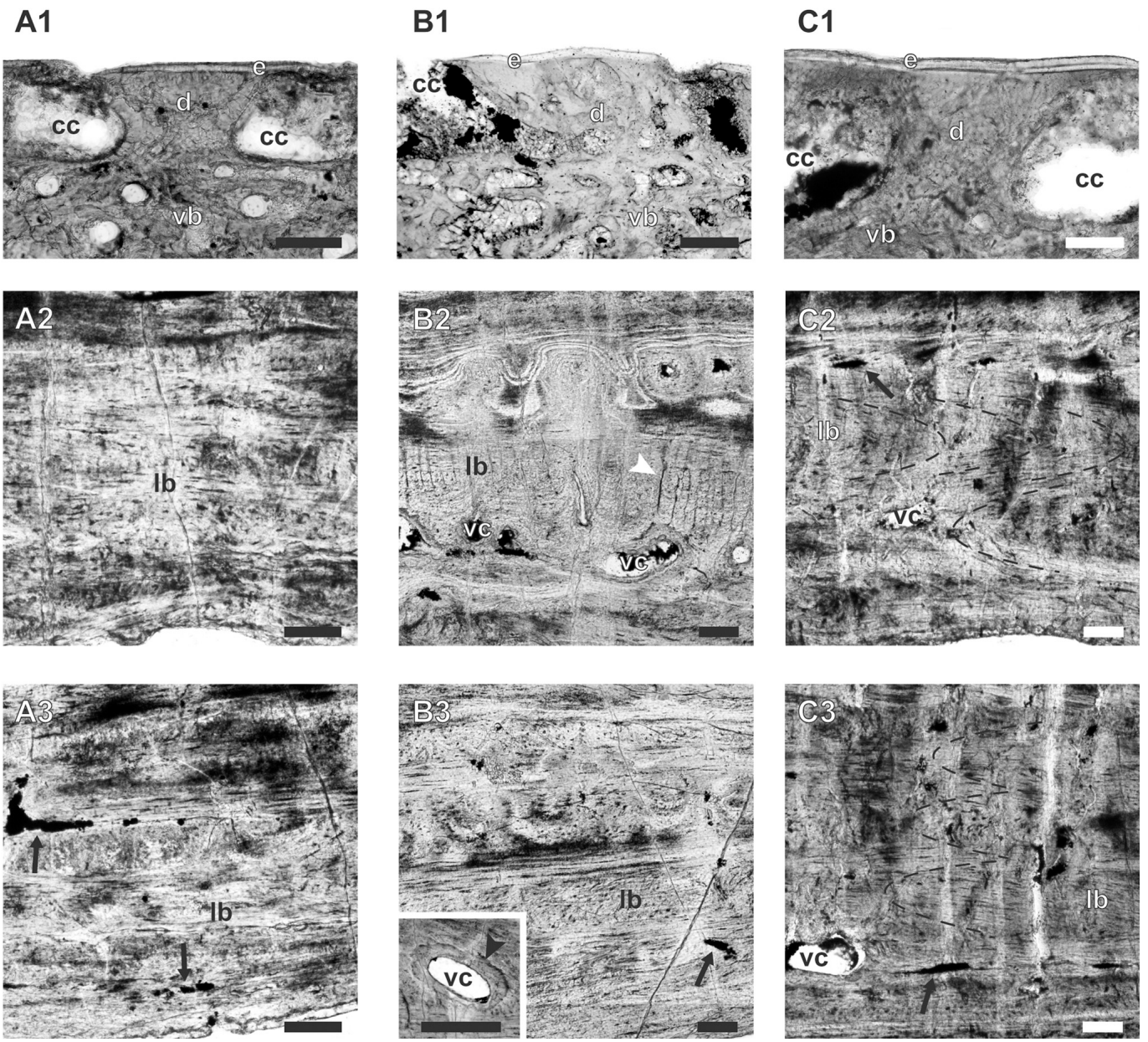


FIGURE 9. Insets of vertical ground sections of *Heimenia ensis* Ørvig, 1969b, isolated scales (see Fig. 8). **A1**–**3**, LIG 45–2042 (rhombic morphotype); **B1**–**3**, LIG 45–2045 (intermediate morphotype); **C1**–**3**, LIG 45–2050 (rounded morphotype). **A1**, **B1**, and **C1**, superficial part of the scales showing the enamel, dentine, and upper parts of the middle vascular bone layer. Note the presence of the characteristic cosmine canals in the dentine and the absence of enamel lining on the inner walls of the canals. **A2**–**3, B2**–**3**, and **C2**–**3**, internal part of the scales showing the arrangement of the collagen plies in the basal lamellar bone layer (isopedine). Note the orthogonal arrangement of the collagen plies in the rhombic (**A2**–**3**) and intermediate (**B2**–**3**) scales, and the twisted arrangement of the collagen plies in the rounded scales (**C2**–**3**). Black arrows point the osteocyte lacunae located between the collagen plies in the basal lamellar bone layer in **A3**, **B3**, **C3**; black arrow head points the resorption line in a secondary osteone of the basal layer in the inset of **B3**; white arrow head points the Sharpey's fibers spreading across the basal layer in **B2**. **Abbreviations**: **cc**, cosmine canal; **d,** dentine; **e**, enamel; **lb**, lamellar bone; **vb**, vascular bone; **vc**, vascular canal. Scale bars equal 100 $\mu$m.

anterior edge, and a field of tubercles located anterior to the cosmine covering), and a derived one known in holoptychiids (e.g., a linear radiation of the dentine tubercles in the anterior exposed area of the scales). As already pointed out by Ørvig (1969a) and Clément (2001), "porolepidids" and holoptychiids have been defined mainly on the basis on scale morphology. Thus, this mix of characters in the *Heimenia* squamation suggests that "porolepidids", as currently defined, could well be paraphyletic.

### Transition from Rhombic to Rounded Scales in Osteichthyans

It is known that transitions from rhombic to rounded scales have occurred independently in several fish lineages: actinopterygians (Schultze, 1966, 1996; Pearson, 1982), dipnoans (Schultze, 1969a), porolepiforms (Ørvig, 1957), and "osteolepiforms" (Jarvik, 1985). In sarcopterygians, both scale types (rhombic and rounded) can be found in a same individual, as described

by Schultze and Heidtke (1986) for a rhizodopsid "osteolepiform", Jarvik (1959) for *Dipterus*, and Ørvig (1969b) for *Heimenia*. However, in *Heimenia*, this transition occurs progressively throughout the body and is not only restricted to the fins as in rhizodopsids (Schultze and Heidtke, 1986) or dipnoans such as *Dipterus* (Jarvik, 1959).

In *Heimenia*, the main morphological changes associated with the transformation from a rhombic to rounded scale shape are due to a differential growth of the anterior and dorsal overlapped areas of the scales, the growth of the cosmine area being isometrically correlated with the general growth of the scale. This condition is different to the one proposed by Jarvik (1980, 1985) for the "osteolepiforms" in which the morphological transformation from a rhombic to rounded shape occurs by the posteriorly and posteroventrally growth of the scales (Fig. 10). Thus, according to Jarvik (1980), the rounded shape of the "osteolepiform" (in fact, tristichopterid) scale is mostly the result of the growth of the exposed area (cosmine area in early "osteolepiforms") in the direction of the overlapped areas of the posterior adjoining scales. However, this scenario is difficult to test in the "osteolepiforms" where no intermediate stages of the transformation from rhombic to rounded scales have been yet found. Thus, it appears that the squamation evolution from rhombic to rounded scales, not only in sarcopterygians but in osteichthyans as a whole, is a clear example of morphological convergence.

Without knowledge of an articulated squamation and assuming that all these different morphotypes of isolated scales (rhombic, intermediate, and rounded) belonged to a single species, namely *Heimenia ensis*, Ørvig (1969b) proposed two explanations for this odd pattern. The first explanation is that rounded, 'holoptychiid-type' scales appear to be a stage in the scale development within the same individual. In this case, a scale ornamented with tubercles in a narrow area of the anterior part of the cosmine could correspond to a stage of resorption period, i.e., a temporary loss of cosmine. Thus, according to Ørvig, *Heimenia* could probably undergo periodic cycles of cosmine resorption and redeposition, like in dipterid lungfishes (Ørvig, 1969a).

The second explanation proposed by Ørvig (1969b) is that the animal presents the two types of scales, rhombic and rounded, at the same time. In this case, a plausible explanation could be the occurrence of a polarity switch in the squamation development in one or more distinct regions of the body and, most certainly, in a specific direction and timing. Ørvig considered that a gradual transition between different scale types occurred and listed the different stages from the anterior to the posterior region in the following order: (1) scales covered with cosmine, rather thick, rhombic, and similar to those of *Porolepis*; (2) scales still covered with cosmine, thinner, tending to be rounded; (3) thin, rounded scales, showing cosmine in the posterior region of its exposed portion and a linear radiation of dentine tubercles in its anterior

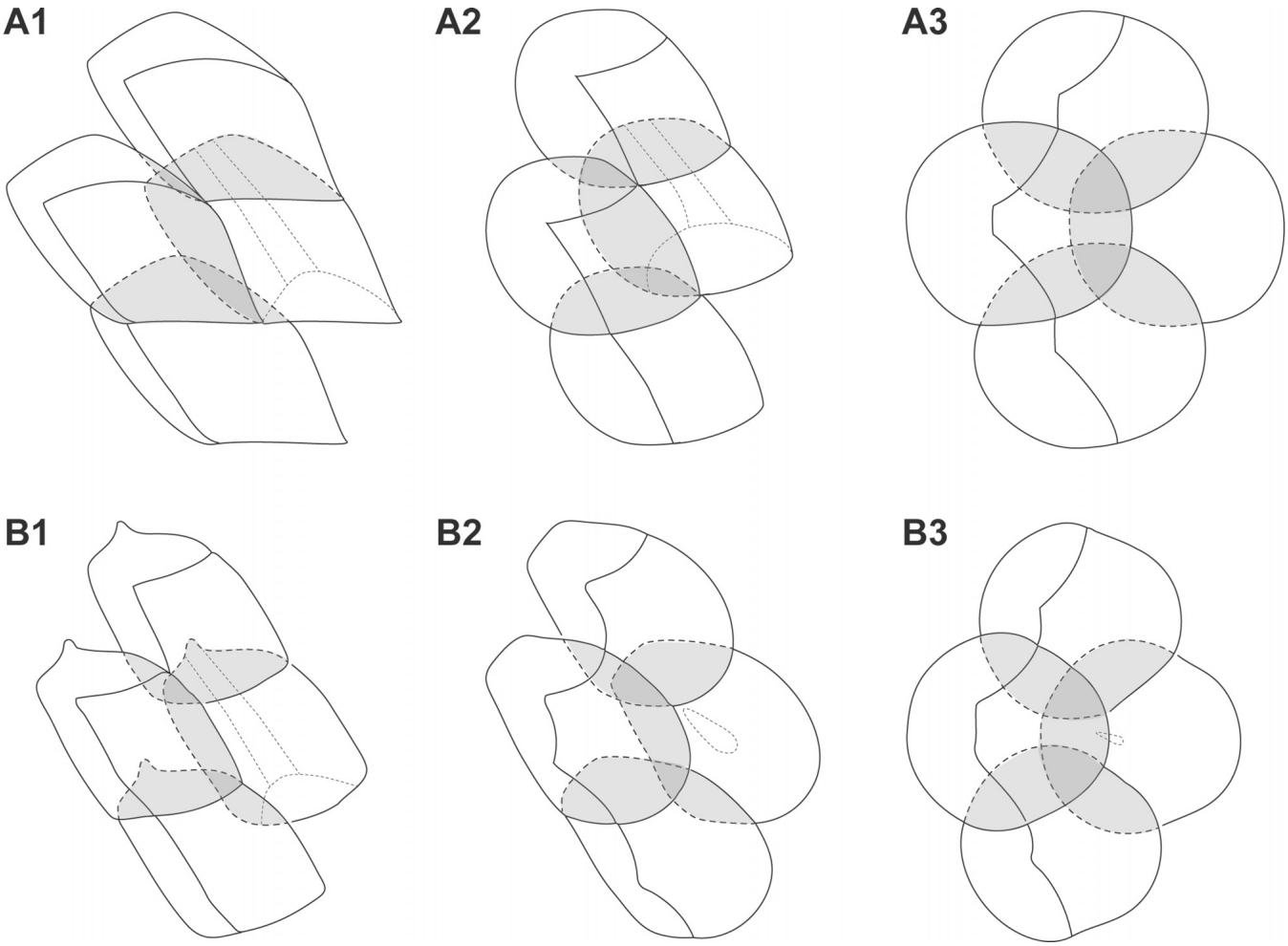


FIGURE 10. Schematic representation of the morphological transition from rhombic to rounded scales in the Porolepiformes (**A1**, *Porolepis*; **A2**, intermediate stage of *Heimenia*; **A3**, *Holoptychius*) and the 'Osteolepiformes' (**B1**, *Osteolepis*; **B2**, putative intermediate stage; **B3**, *Eusthenopteron*). Redrawn and completed after Jarvik (1980). Not to scale.

region; and (4) thin, rounded scales, entirely devoid of cosmine, showing an ornamentation of dentine tubercles similar to those of the holoptychiids.

Ørvig (1969b) assumed that the first observable changes took place in the scales of the caudal region and, subsequently, these changes 'migrated towards' the anterior region of the body. According to this evolutionary pattern, the most rounded scales, thin and lacking cosmine, would be located in the posterior region of the body, whereas the rhombic scales, thick and covered with cosmine, would be located in the anterior region of the body. Furthermore, the pattern of cosmine development in some Devonian dipnoans from Germany (Ørvig, 1960) was also congruent with Ørvig's hypothesis for *Heimenia*: "we first have had cosmine formation on a rather restricted, anterior group of ventral scales somewhere behind the gular plates and that this subsequently spread to other scales, fairly rapidly to those lying behind but also, more slowly, to those following in a lateral direction" (Ørvig, 1969a:250).

The polarity pattern seen in the squamation of the nearly complete new *Heimenia* body is actually reversed from the assumptions made by Ørvig (Figs. 3, 4). However, according to Ørvig's scenario, cosmine should not be found in the last phylogenetic stage of his hypothetical scale development (the putative stage 4). Albeit the fact that in the nearly complete specimen cosmine has been generally lost during fossilization, all the large and rounded isolated scales always show cosmine patches on their external surface. It seems that the complete loss of cosmine associated with the well-developed rounded shape of the scales did not occur in *Heimenia*.

Dorsal pegs and articular ridges (or keel) on the internal surface of the *Heimenia* scales are also known in the scales of *Porolepis* (Gross, 1966), "osteolepidids" (Jarvik, 1985), and 'elpistostegalians' (Witzmann, 2011). A 'peg-and-socket' articulation associated with an articular ridge is considered to be a primitive character for osteichthyans (Friedman and Brazeau, 2010). In *Heimenia*, the articular ridge becomes partly reduced in the intermediate scales and disappears completely in the rounded scales, a condition seen in the large rounded scales of holoptychiids such as *Laccognathus* or *Holoptychius*. The disappearance of the keel in *Heimenia* and holoptychiids is also convergent with the condition seen in rhizodontids and tristichopterids where it appears to be absent (Jarvik, 1948, 1950, 1985). However, Jarvik proposed that in those groups the inner keel was transformed into a characteristic teardrop-shaped boss. The "osteolepiform" *Litoptychus* seems to be an exception in "osteolepiforms" because there is no trace of a boss in the internal surface of its rhombic scales (Coates and Friedman, 2010).

Three examples of squamation showing rhombic and rounded scales in the same specimen have been found in the literature for fossil osteichthyans: two Mesozoic actinopterygians and a Permian rhizodopsid "osteolepiform." The actinopterygian *Coccolepis bucklandi* from the Upper Jurassic of Bavaria (Schultze, 1996:fig. 4) has ganoid rhombic scales on its caudal peduncle and rounded scales of amioïd-type located anteriorly. The transition between both types of scales is abrupt and perfectly defined; both shapes (rhombic and rounded) are present on a single vertical scale row. The actinopterygian *Propterus microstomus* from the Upper Jurassic of Bavaria (Schultze, 1966:fig. 31) also has rhombic scales in the posterior region and rounded scales in the anterior region of the body; the transition, nonetheless, is much more gradual between them. The rhizodopsid "osteolepiform" from the Permian of Germany (Schultze and Heidtke, 1986:figs. 1–2) shows a remarkable combination of rounded scales on the body and rhombic scales on the fin lobes (at least on the pelvic fins).

These examples support the hypothesis that derived character states related to squamation in osteichthyans generally begin in the anterior region, whereas the rear and fin regions retain the primitive states (Coates, 1994). It is also plausible that intermediate stages, similar to those seen in *Heimenia*, could be found in new fossil discoveries among other groups of Devonian sarcopterygians where this transition from rhombic to rounded scales also occurs (i.e., lungfishes, "osteolepiforms", and possibly tetrapods—but see Witzmann, 2011, for another interpretation concerning the latter).

### Squamation Evolution in the Porolepiformes

The scale morphology of the new *Heimenia* material is quite similar to that of *Porolepis* cf. *elongata* (Jessen, 1989) and *Porolepis* ex grege *posnaniensis* (Kulczycki, 1960). As Ørvig (1969b:286) suggested, "it is possible that the material, including scales, described as *Porolepis* ex grege *posnaniensis* by Kulczycki (1960) from the Emsian beds of the Holy Cross Mountains in Poland, belongs to *Heimenia*."

The internal surface of the *Heimenia* scales presents a concave area (i.e., the 'socket'). This depression, well delimited in the rhombic and intermediate scales, becomes larger and anterodorsally developed in the rounded scales, occupying the greatest part of the internal surface of the scales. The slight groove seen in the rounded scales of *Heimenia* is the only remnant of the primitive 'peg-and-socket' articulation of the rhombic scales, a condition known in "osteolepidids" and rhombic-scaled actinopterygians. The rounded and ovoid scales of the holoptychiids show no trace of this overlapping area. This condition corroborates the interpretation of the scale morphology of *Heimenia* as 'intermediate' between those of *Porolepis* and the holoptychiids.

The number of scale rows in *Heimenia* (around 40 from the cleithrum to the base of the caudal peduncle) is close to that of *Porolepis* (around 45). The holoptychiids have a number of scale rows equal or inferior to that of "porolepidids": around 30 in *Quebecius* (Cloutier and Schultze, 1996), and 28 in *Holoptychius* (Jarvik, 1980; Cloutier and Schultze, 1996). In *Heimenia*, the two dorsal fins are separated by seven or eight scale rows of scales, as in *Porolepis*. This number is divided by two in the holoptychiids.

According to the reconstruction of *Porolepis* (Clément, 2004), in *Heimenia* the number of scales per row is relatively similar (about 20 on each side). In the holoptychiids, this number is also divided by two due to the greater size of the rounded scales in comparison with the small rhombic scales of the "porolepidids". Although the number of scale rows and the number of scales per row in *Heimenia* are very similar to those observed in *Porolepis*, the rounded scales of *Heimenia* are substantially larger than the rhombic scales located in the same position in a specimen of *Porolepis* of similar size (J. M.-F. pers. observ.). However, they are not as large as the rounded scales from the same region of similarly sized holoptychiids such as *Holoptychius* (Cloutier and Schultze, 1996; J. M.-F. pers. observ.).

In *Heimenia*, there is no evidence of a 'ventrolateral ridge' or 'inversion scales' in the flanks as those described by Jarvik (1948, 1985) in the "osteolepidids" and by Witzmann (2011) in *Panderichthys*. The arrangement of the scales is more similar to what can be seen in the rhombic squamation of the lepisosteid actinopterygians (e.g., Grande, 2010). Thus, in sarcopterygians the differentiation between ventral (sometimes so-called 'gastral') and dorsal scales appears to be a synapomorphy of the Tetrapodomorpha, with the possible exception of rhizodontids (see Witzmann, 2011). This marked regionalization of the squamation in flank and ventral scales in tetrapodomorphs is not present in the Porolepiformes, nor in Dipnoi, hence not in the Dipnomorpha as a whole (Ahlberg, 1991).

### Histology

The histological differences among teeth, dermal bones, and scales of lungfishes, "osteolepidids", and "porolepidids" are well

known, given studies by Bystrow (1939), Gross (1936, 1956, 1966), and Schultze (1969b, 1970, 1977), among others. Cosmine and cosmine function has also been described by Thomson (1975, and references therein), Meinke (1984), and Borgen (1989, 1992). It is not in the scope of this study to refute or propose an explanation of the function of the pore-canal system of the cosmine in the porolepiforms, or in sarcopterygians. We will limit our interpretations to the microstructural differences of the cosmine and other histological structures of the Porolepiformes scales.

The oldest occurrence of cosmine in the stem sarcopterygian fish *Meemannia eos* indicates that cosmine in crown-group sarcopterygians might have developed step by step, first through the acquisition of a pore-canal network (in *Meemannia*) and subsequently through the development of an increased ability to resorb previously deposited enamel-covered odontode layers (as in *Psarolepis*, *Styloichthys*, and crown-group sarcopterygians) (Zhu et al., 2006, 2010). Ørvig (1969a) considered that there was no complete resorption of the cosmine in the Porolepiformes, although resorption may have occurred in the ontogenetic stage where only odontodes formed, prior to the definitive deposition of the cosmine. This pattern would explain the presence of free odontodes enclosed below the dentine layer in "porolepidids" such as *Porolepis* (Gross, 1936, 1956, 1966) but also in the basal lungfish *Uranolophus* (Denison, 1968a, 1968b). In *Heimenia*, there is no trace of older odontodes below the cosmine layer.

The occurrence of several superimposed odontodes embedded in the vascular bone middle layer has been reported in *Porolepis* and in the holoptychiids *Laccognathus* and *Glyptolepis* (Bystrow, 1939; Gross, 1966; Ørvig, 1968; Sire et al., 2009). This character seems to be very plastic among the Porolepiformes and thus cannot be used to separate "porolepidids" from holoptychiids. Their absence in *Heimenia* can be considered as an autapomorphy of the genus and can be explained either by the fact that the cosmine and the anterior tubercles in the *Heimenia* scales correspond to the first generation of cosmine deposition (in this very improbable case, all the isolated *Heimenia* scales would correspond to a juvenile state); or by the occurrence of complete resorption of previous odontode generations. We prefer the latter explanation, because our histological ground sections show no distinct separation between the anterior region of the cosmine, where free dentine tubercles develop, and the continuous cosmine covering of the exposed area of the scales.

The free tubercles located anterior to the cosmine are slightly concave in their upper surface and show a characteristic spoon or horseshoe-like shape (Ørvig, 1969b), similar to those of the holoptychiids (Ørvig, 1957), onychodontids (Andrews et al., 2006), Devonian coelacanths (Forey et al., 2000), and early lungfishes (Denison, 1968a, 1968b). Ørvig (1969a) and Meinke (1984) proposed that in the Porolepiformes, the free tubercles in the anterior part of the cosmine very probably represented the peripheral part of an odontode layer belonging to an earlier growth stage than the cosmine itself. However, a close observation of those denticles in the new *Heimenia* material refutes this interpretation. Some partially isolated tubercles are covered by enamel, and in some cases, the enamel of the odontode is still attached to the continuous enamel layer of the rest of the cosmine covering of the exposed area.

The morphology of those isolated odontodes seems to correspond to a stage of partial resorption of the cosmine, a condition similar to that described by Thomson (1975) for the scales of *Ectosteorachis* and *Megalichthys* and by Borgen (1989) in the lower jaws of *Gyroptychius* and *Megalichthys*, in which the enlargement of the cosmine pores leads to the formation of dentine islets that may or may not be covered by enamel. This condition was called 'incomplete resorption' by Borgen (1989, 1992). Moreover, to Borgen (1989:414), "the areas with this configuration seem mostly to be situated at a deeper level than the surfaces both of the normal cosmine and the enlarged pores." This condition would explain the statements made by Ørvig (1969a, 1969b) and Meinke (1984), according to which the deeper disposition of the tubercles was assumed to be due to an older generation of odontodes. Thus Ørvig's first interpretation of the peculiar squamation of *Heimenia* (see above) could be partly confirmed, because a resorption process is considered to be possible in the anterior part of the cosmine. However, such resorption process leading to a complete loss of the cosmine does not concern the entire surface of the scale, or the squamation, as proposed by Ørvig (1969b). In *Heimenia*, the resorption of the cosmine is restricted to the anterodorsal margins of the cosmine, i.e., the posterior-most region of the overlapped area of the scale.

The anterior and dorsal margins of the cosmine covering of the *Heimenia* scales show a characteristic elongated ridge system. These ridges seem thinner and more abundant than in *Porolepis* (J. M.-F. pers. observ.). Following the pattern proposed by Borgen (1989), the presence of ridges in the anterior and dorsal parts of the cosmine could be considered as a result of the enlargement of the cosmine pores and subsequent fusion of cosmine-less areas, resulting in the formation of ridges bordering those areas. In fact, the diameter of the cosmine pores in *Heimenia* increases gradually towards the anterior and dorsal borders of the cosmine. The thinning of the ridges in *Heimenia*, compared to the thicker ridges of *Porolepis*, could be interpreted as a more advanced state in the resorption of the cosmine margins, in which the cosmine-less areas are larger than in *Porolepis*.

This resorption and development pattern of ridges and isolated tubercles in the anterior and dorsal margins of the cosmine in the Porolepiformes can be applied not only to *Heimenia*, but also to other porolepiforms in which free tubercles are also present. The formation of tubercles in this area is consistent with the function of isolated tubercles as a reinforcement of the adhesion properties between the scales and the overlying epithelium, thus reducing internal friction between scales at this level (see Burdak, 1979, and references therein). In holoptychiids such as *Glyptolepis* and *Laccognathus*, isolated tubercles are not restricted to the overlapped areas but distributed throughout the exposed area of the scales (Downs et al., 2011). However, the origin of those isolated tubercles in holoptychiids seems to be more complicated than a mere partial resorption process and needs further histological investigation.

Histological thin sections of our new isolated scale material confirm that the substance overlying the dentine is true enamel and not enameloid, and that the inner walls of almost all the canals show a 'bulged' layer than can be mistaken with an enamel layer (Fig. 9A1, B1, C1), but clearly there is no enamel lining on these walls. These observations refute the assumptions made by Ørvig (1969b) and Meinke (1984) concerning the enamel lining of the inner walls of the pore-canal system in *Heimenia*. Moreover, Ørvig did not provide any histological section of the *Heimenia* type scales to support this assumption. A close observation shows that this layer is in fact a decomposition front of the dentine made by fungi, surely post mortem, or due to the action of the formic acid during preparation of our scales. An enamel lining of the pore-canal system is present in *Porolepis*. Its absence in *Heimenia* could represent an early stage towards the break-up of the cosmine in porolepiforms.

A key feature in the evolution of scale structure between "porolepidids" and holoptychiids is related to the organization of the basal lamellar bone layer, i.e., isopedine sensu Francillon-Viellot et al. (1990) and Meunier (1987). In relation to this, Ørvig (1969b:290) stated that the scales of *Heimenia* approached the condition of holoptychiid scales by "their decrease in thickness, effected by a reduction of the basal bone tissue with the result that the successive bone-laminae added to the basal face during the growth in cases only appear as peripheral annulae, and [. . .] the development in them of a flat or concave basal face with a vestigial remnant of an oblique ridge or no such ridge at all, and

no distinctly marked-off overlapping areas either, even these features tied up with processes of reduction in the basal bone tissue." Our general observations of the new *Heimenia* scales are consistent with Ørvig's interpretation; however, when histological data are considered, our conclusions differ from Ørvig's. The decrease in absolute scale thickness from rhombic to rounded scales in *Heimenia* seems to be due to the relative thinning of the middle vascular bone and dentine layers compared to the thickness of the basal bony layer (Fig. 8) and not to a reduction of the basal bony layer, as considered by Ørvig. Moreover, the elongation of the internal keel seen in the intermediate and rounded scales could explain the increase of the relative thickness of the basal bone layer (isopedine and internal bone layer forming the keel) relative to the cosmine and vascular bone layers in the intermediate and rounded scales.

Another condition in the *Heimenia* scales approaching that of the holoptychiids concerns the orientation of the collagen plies in the isopedine layer. In the rhombic scales, the collagen plies are generally arranged orthogonally, whereas in the intermediate and especially in the rounded scales, the orientation of the plies varies, almost reaching a twisted plywood structure, similar to that seen in the isopedine layer of the rounded scales of *Holoptychius* (pers. observ.) and *Eusthenopteron* (Zylberberg et al., 2010) and in the elasmodine layer of *Latimeria* (Giraud et al., 1978).

### *Heimenia* Paleoecology and Morphofunctional Interpretation of the Squamation

Thick and densely mineralized scales (e.g., rhombic cosmoid scales) are often related to stiffness of the body and help 'armored' fishes to cope with the mechanical constraints of the aquatic environment. On the other hand, thin and lightly mineralized scales (e.g., rounded elasmoid scales) increase flexibility and are often characteristic of agile fishes. The rhomboid squamation of the early sarcopterygians is consistent with their representation as nectobenthonic fishes, incapable of reaching high speeds during swimming (Burdak, 1979). Despite the fact that primitive osteichthyans and sarcopterygians are classically considered as less efficient swimmers than derived actinopterygians (e.g., teleosts), the squamation and disposition of the median fins would have provided a wider range of morphofunctional solutions to different types of swimming (see Belles-Isles, 1992). This combination of features should not be regarded as necessarily 'primitive' but, rather, different and/or alternative to different life conditions and aquatic locomotions (see examples for lepisosteids and polypterids in Gemballa and Bartsch, 2002).

It is known that the presence of an articular ridge on the internal surface of the osteichthyan scales, associated with the 'peg-and-socket' articulation, allows resisting compressive and tensile strain along the oblique scale rows axis (Gemballa and Bartsch, 2002). The presence of Sharpey's fibers connected to the keel strengthens the union between lateral adjoining scales, as well as with those of the same row. Rotation of the scales around the 'peg-and-socket' articulation is made impossible by this construction, thus limiting the degree of trunk flexibility in the vertical plane (Burdak, 1979) but allowing lateral flexions (Pridmore and Barwick, 1993; Gemballa and Bartsch, 2002). The disappearance of this keel in the rounded scales enables the scales to slide over each other more easily, enhancing flexibility and allowing the trunk to bend, not only laterally but also vertically (Pearson, 1982).

A closer look at the overlapping pattern of the *Heimenia* squamation shows that each rounded scale of the anterior region of the body is surrounded by, and in contact with, eight scales but partially overlapped only by three scales (Figs. 3, 4, 10A2). This condition is different to the thick and greatly overlapped pattern present in lungfishes (Pridmore and Barwick, 1993) and matches more closely the pattern of the rounded-scaled actinopterygians (Burdak, 1979). Indeed, trunk flexibility is not only related to the presence of rounded scales but also to a lesser degree of overlapping of the scales, and to a lower body thickness invested by scales in transverse section.

"Porolepidids" are considered as fully marine or near shore inhabitants, whereas the holoptychiids are regarded as more fresh water or marginal marine dwellers (Ahlberg, 1992b). The fusiform and elongated body of the "porolepidids", combined with the lack of large anterior fins, could have allowed wide and rapid lateral movements of the anterior portion of the body (see Webb and Skadsen, 1979; Webb, 1984). It is also known that the porolepiform body was adapted to a considerable degree of yaw (lateral movements of the anterior part of the body). Such body configuration suggests that the Porolepiformes were capable of performing a combination of high maneuverability and relatively high acceleration, rather than solely maximize acceleration (Ahlberg, 1992b).

In *Heimenia*, the presence of rounded scales in the most anterior part of the body is here regarded as an adaptation to a more dynamic and agile life style (Fig. 11). The anterior region of the body covered by rounded scales, immediately behind the head, could thus have performed tight and sudden turns during predation on a wider range of angles than only laterally. The posterior region of the body covered by rhombic scales could have produced the main thrust during locomotion, thus corresponding to the carangiform to subcarangiform swimming style (Lindsey, 1978; Webb, 1984). This body configuration is congruent with the representation of the "porolepidids" as ambush predators (Ahlberg, 1992b; Clément, 2004).

Moreover, the sensory line system in the Porolepiformes is strongly developed in the head, whereas the lateral line system is less developed. This pattern is consistent with the proposed ecology of the Porolepiformes as predatory fishes of dark or murky waters (Ahlberg, 1992b; Clément, 2004). In "porolepidids" such as *Porolepis* and *Heimenia*, the combination of a highly developed sensory line system in the skull (Clément and Ahlberg, 2010), the restricted mobility of the pectoral fins in a vertical plane (Ahlberg, 1989), and the thick, rhomboid squamation, not only in the rear of the body but also in the ventral region, are good examples for a quasi-benthic mode of life in primitive porolepiforms (see Ahlberg, 1989, 1992b; Clément, 2004).

In holoptychiids, such as *Holoptychius* or *Quebecius*, rounded scales cover the entire body (Cloutier and Schultze, 1996). According to the generally accepted evolutionary pattern concerning the spread of the derived characters from the anterior to the posterior region in fishes (Coates, 1994), it could be proposed that in the Porolepiformes the extension of rounded scales all over the body began in the anterior region, probably as an adaptation to enhance flexibility of the anterior portion of the body. The complete covering of the body by rounded scales could have been the result of an increase of the flexibility of the fish and the loss of a strictly benthic lifestyle. This morphological evolution could also be related to the change in the life habits of the Porolepiformes during the Middle-Late Devonian in which the more fresh water environments were preferably occupied by the holoptychiids, in contrast to the fully marine or near-shore environments associated to the presence of "porolepidids".

Surprisingly, a squamation pattern similar to that of *Heimenia* was described for the tuna fish *Thunnus alalunga* by Meunier and Sire (1981), in which the overall shape of the elasmoid scales shows a gradual transition from the anterior, rounded scales, to the posterior, more or less squared scales. In the case of *Thunnus*, this pattern is strongly associated with a gain of speed during swimming, the squamation of the tuna fish being a classical example of an adaptation to sustained high speed cruising swimming. In the case of *Heimenia*, and other Porolepiformes, the squamation and body design were not adapted to a steady swimming, as in *Thunnus*, but rather to an unsteady

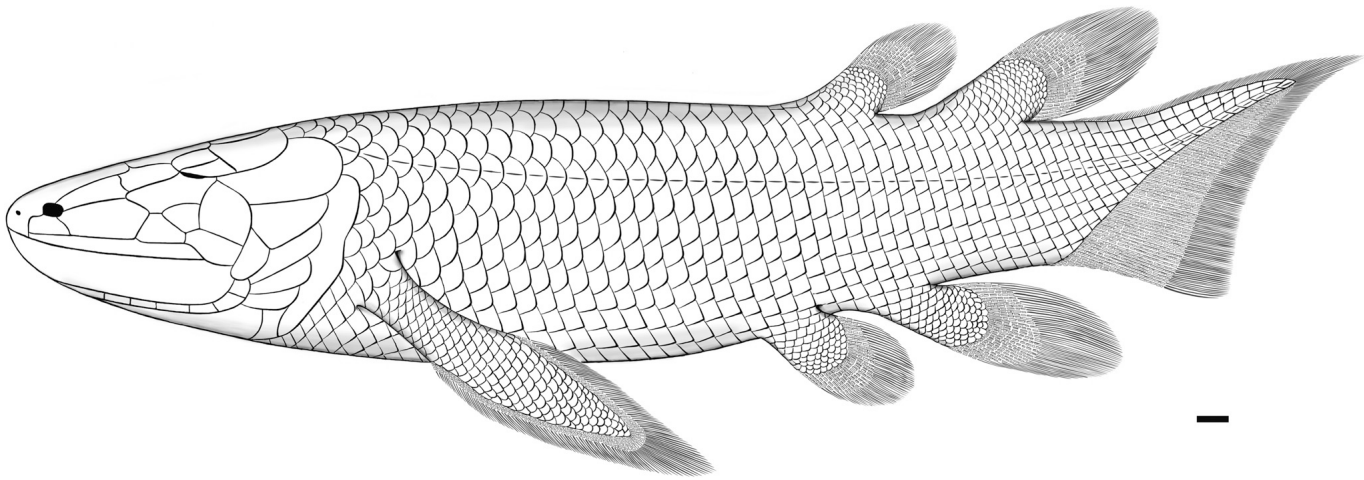

FIGURE 11. Interpretative reconstruction of *Heimenia ensis* Ørvig, 1969b. Postcranial morphology based on specimen LIG 45–2027 (nearly complete body) and head morphology based on specimen LIG 45–2001 (cranial remains described by Clément, 2001), and *Porolepis* as in Clément (2004). Scale bar equals 1 cm.

swimming, in which acceleration and rapid maneuvering were more suited to their mode of life.

## CONCLUSION

Our new observations of the *Heimenia* squamation confirm some of the ideas proposed by Ørvig (1969b) but refute others. Resuming Ørvig's assertions concerning the specialization of *Heimenia* scales towards the condition of holoptychiids, we list the following: (1) tendency to the gain of a rounded shape; (2) presence of well-developed overlapped areas; (3) development of a flat or concave internal surface, with a vestigial remnant of an articular ridge, or its disappearance; (4) twisted orientation of the collagen plies in the isopedine layer; and (5) decrease in general thickness, related to the reduction of the middle vascular bone and dentine (cosmine) layers.

Concerning the latter, the decrease in absolute thickness from rhombic to rounded scales is due to the relative thinning of the middle vascular bone and dentine layers compared to the thickness of the basal bony layer and not to a reduction of the basal bony layer alone, as considered by Ørvig. Moreover, the morphological transformation from rhombic to rounded scales in *Heimenia* seems to be related to a pronounced growth of the anterior and dorsal overlapped areas of the scales, in which the anterior margin acquires a rounded outline before the posterior one.

According to Ørvig (1969a), phyletic changes such as the transition from rhombic to rounded scales in the Porolepiformes, the flattening of the internal surface of the scales and the reduction, and subsequent disappearance of the cosmine did not initially affect the squamation as a whole, but may have originated in certain parts of the body and successively spread to others. Our results confirm that although Ørvig's interpretation was correct, the pattern of transformation from rhombic to rounded scales and the direction of the spreading could have taken place from the anterior to the posterior region of the body, as it is shown in *Heimenia* where rounded scales are found in the front and rhombic scales are located in the rear. The transition from generalized scale morphology (rhombic) to a derived one (rounded) could be the result of still unknown developmental processes occurring during ontogeny under the selective pressures of functional adaptations. In the case of the porolepiforms and stem tetrapodomorphs, the general condition still corresponds to the evolutionary advantage of the anterior portion of the body against the posterior one, thus adding a new example to support the hypothesis of the anteroposterior spread of derived characters in fishes (Coates, 1994). The differentiation between ventral ('gastral') and dorsal scales appears to be a synapomorphy of the tetrapodomorph sarcopterygians.

Finally, concerning the two families among the Porolepiformes ('Porolepididae' and Holoptychiidae), and the intermediate condition of *Heimenia*, Ørvig (1969b:294) stated that "the distinction between them would not any longer rest on the scales being rhombic or cycloid [sic], but on whether the scales in any part of the squamation still retain a cosmine layer [in the 'Porolepididae'] or have lost this layer [in the Holoptychiidae]."

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## A HOLOPTYCHIID POROLEPIFORM (SARCOPTERYGII, DIPNOMORPHA) FROM THE FRASNIAN OF COLOMBIA, WITH REMARKS ON THE LATE DEVONIAN EURAMERICA-GONDWANA VERTEBRATE FAUNAL INTERCHANGE

The Paleozoic fish faunas of South America have been thoroughly studied by Philippe JANVIER (see reviews in JANVIER, 2007a; JANVIER & MAISEY, 2010). The evolutionary and paleobiogeographical implications of these faunas have proven to be essential in our understanding of fish distribution and continental arrangement in the Devonian. However, there are still certain taxonomical and paleobiogeographical aspects that need to be precised and evaluated in the light of unusual discoveries. This was the case of the putative occurrence of holoptychiid porolepiforms, a widespread but endemic group of Euramerican sarcopterygians, in the Late Devonian (Frasnian) of the North-western margin of Gondwana, corresponding to today's location of Colombia.

During his numerous field trips in Central South America in the 2000's, Philippe JANVIER found a sarcopterygian tooth fragment in the Potrero Rincón locality of Colombia. Based on the dendrodont structure of its plicidentine, he assigned it to an undetermined holoptychiid porolepiform (JANVIER & MAISEY, 2010: 435) that completed the former record of isolated "*Holoptychius*-like" scales from the same site (JANVIER & VILLARROEL, 1998, 2000). However, the former attribution of this tooth had not been published nor confirmed by further histological survey. When he proposed me to work on these fossil remains, I seized the chance to restudy all the putative holoptychiid material from the Potrero Rincón fossil site housed in the MNHN. This material comprises the tooth fragment, several isolated scales, and a skull roof bone of an undetermined sarcopterygian that could possibly be a holoptychiid porolepiform.

Two cross sections of the basal portion of the tooth had already been performed before I began this study but had not been properly observed nor illustrated in order to fully describe its microstructure. The skull roof bone was slightly mechanically prepared to free the natural margins of the bone from the matrix but due to its extreme fragility it was not possible to produce casts. Several elastomer casts were produced from the highly eroded negative mould of the rest of the tooth and scale remains. All remains were newly photographed in the MNHN.

Though not directly related to the main subject of this thesis (i.e., scales and fin rays), teeth histology in sarcopterygians deserves a special mention. Indeed, sarcopterygians show a large set of different arrangement of their teeth dentine, and for most of them, the folding of the plicidentine has a systematic interest. Leaving aside the dipnoans, which have highly specialized dentary crushing plates (SMITH, 1984), four types of tooth organization may be observed in sarcopterygians (SCHULTZE, 1969b, 1970) (see Fig. II.1 for anatomical references):

**A**. *Simple Teeth.* The pulp cavity is free and there are hardly any dentine folds. Simple teeth are observed in coelacanths (e.g., *Latimeria* in CASTANET *et al.*, 1975*)* and onychodontids (e.g., *Onychodus* in SCHULTZE, 1969b). Dipnoans also show simple teeth, but it is considered a reversion from a plicated condition present in basal members (VOROBYEVA, 1977a; JANVIER, 1996).

**B.** *Polyplocodont Teeth.* Polyplocodont teeth have a pulp cavity. The orthodentine organizes as a plicidentine; it develops folds that are oriented centripetally, towards the middle of the pulp cavity. These first-order folds remain rather simple but second-order ones can develop on them. Bone of attachment spreads between the external folds at the base of the tooth. Polyplocodont folding is a primitive and rather common feature of sarcopterygians. It is present in the stem sarcopterygian *Psarolepis* (YU, 1998; ZHU *et al.*,

1999), stem dipnomorphs (e.g., *Youngolepis* and *Powichthys*) (CHANG & SMITH, 1992; CLÉMENT & JANVIER, 2004), most "osteolepiforms" (e.g., *Eusthenopteron*), "elpistostegalians" (e.g., *Panderichthys*) and in tetrapods (e.g., *Ichthyostega* and Carboniferous loxommatids) where it is called labyrinthodont plicidentine (SCHULTZE, 1969b). Therefore polyplocodont plicidentine does not constitute a strong argument for inferring close phylogenetic relationships. Moreover, "osteolepiforms" also have small non plicated teeth (e.g., dentary teeth).

**C.** *Eusthenodont Teeth.* In these teeth the pulp cavity is more or less filled by osteodentine. The folds of plicidentine are more complex and are rather numerous. Attachment bone spreads between external folds. The eusthenodont tooth is a moderately advanced type of folded tooth known to occur only in *Eusthenodon, Litoptychus* and *Platycephalichthys* (SCHULTZE, 1969b). But, as for polyplocodont folding, eusthenodont plicidentine does not imply close phylogenetic relationship of these taxa.

**D.** *Dendrodont teeth.* In dendrodont teeth the pulp cavity is filled by osteodentine. Plicidentine forms highly complex and regular folds. Attachment bone is restricted to the base of the tooth and does not spread between external folds. The dendrodont plicidentine is considered an autopomorphy unique to porolepiforms and is certainly derived from the polyplocodont folding present in stem dipnomorphs (e.g., *Youngolepis* and *Powichthys*).

The presence of dendrodont plicidentine in our isolated Colombian tooth has proven to be crucial in its attribution to the Holoptychiidae (see Paper II for further details). I also studied two tooth cross sections of another porolepiform, the "porolepidid" *Heimenia ensis* and it revealed to possess the expected dendront plicidentine (Fig. II.2, compare it with Fig. 3 in Paper II).

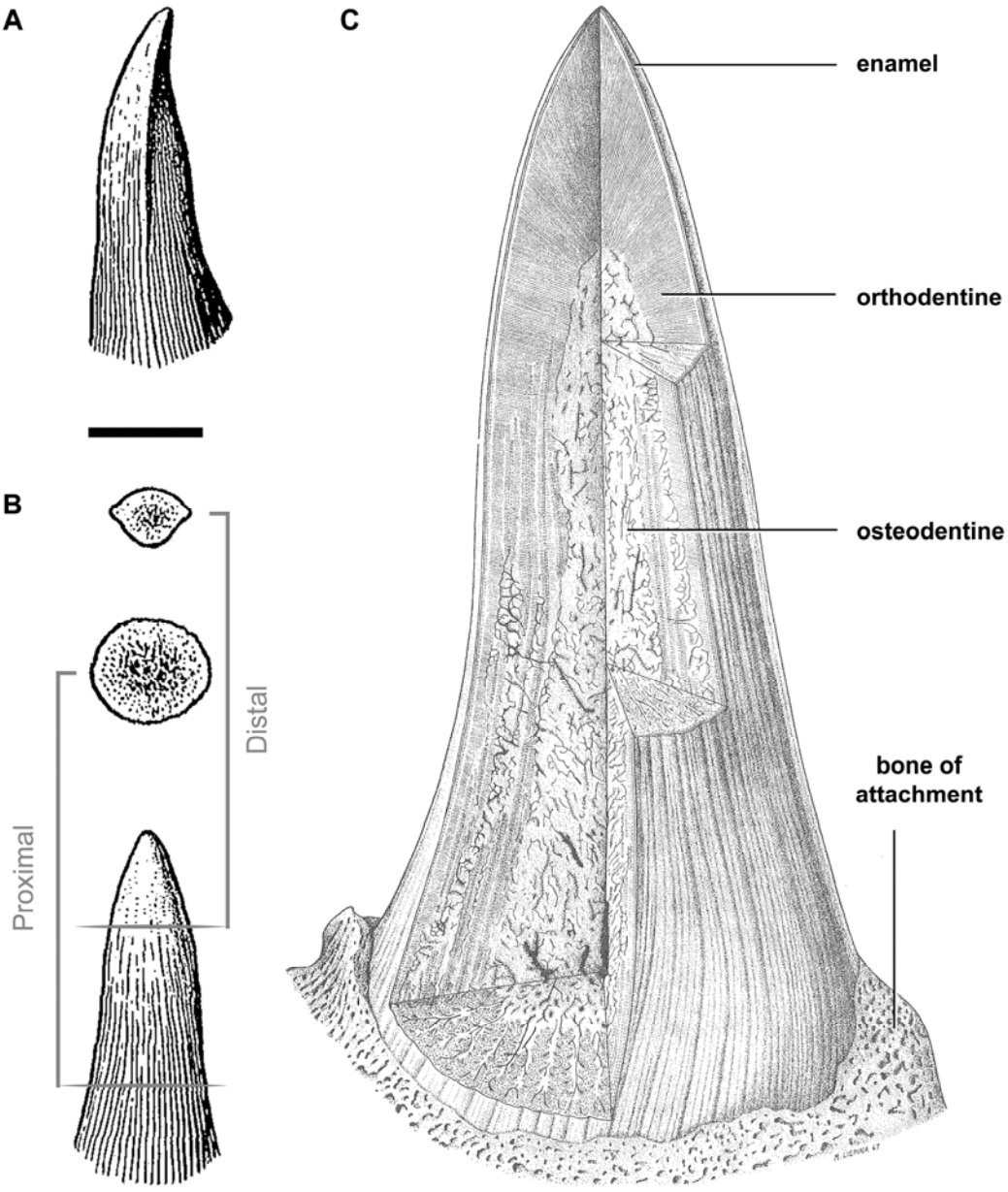


**FIGURE II.1. Nomenclatural basis for microstructural porolepiform tooth description** (e.g., *Laccognathus*). **A.** Frontal view of an isolated tooth, note the presence of the cutting carina in the lateral (front) margin. **B.** Guide to the location of proximal and distal cross sections in a tooth in labial view, note that the presence of mesial carinas is only visible in the distal half of the tooth. **C**. Reconstruction of the internal structure of a dendrodont porolepiform tooth. Modified after BYSTROW, 1939 (A,B) and SCHULTZE, 1969b (C). Scale bar equals 1 cm.

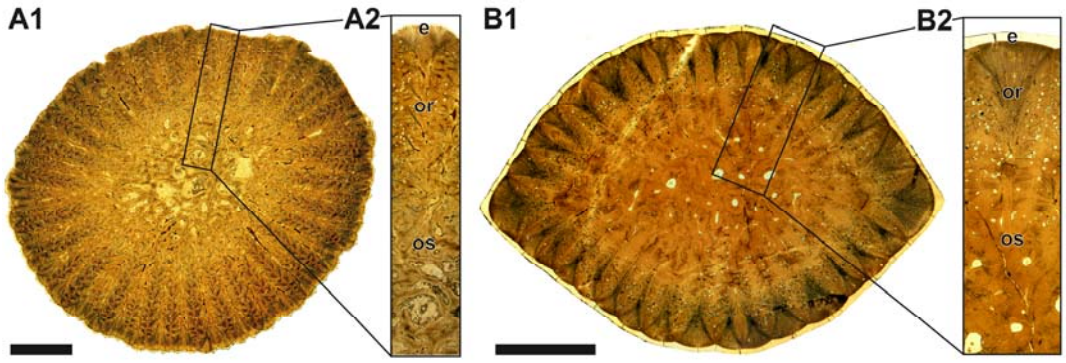


**FIGURE II.2. *Heimenia ensis* tooth cross sections. A.** Proximal section near the base of the tooth, **A1.** General view, **A2**. Inset showing the arrangement of, from external to internal, enamel, orthodentine (dendrodont plicidentine), and osteodentine. **B**. Distal section at mid height of the tooth. Note the presence of cutting carinas in both mesial margins, **B1**. General view, **B2**. Inset showing the arrangement of, from external to internal, enamel, orthodentine and osteodentine. Note that the dendrodont pattern is less marked than in the proximal cross section and the well-visible dentinal tubules). **Abbreviations: e**, enamel; **or**, orthodentine; **os**, osteodentine. Scale bars equal 1 mm.

Another important issue that was highlighted by this study concerns the renewed importance of the scales as a valid taxonomic feature. I have become aware that although the scales of Devonian sarcopterygians show a high rate of morphological convergence, the systematic attribution of isolated scales to certain taxa (e.g., group, family, genus, or even species) must no longer rest on general appearance or overall ornamentation, but rather on a combination of as many key characters as possible. These features are in the vast majority of cases only external, i.e., shape and ornamentation of the external or internal surfaces, but histology can settled this because histological characters are very distinctive between different groups, independently of the external morphological convergences.

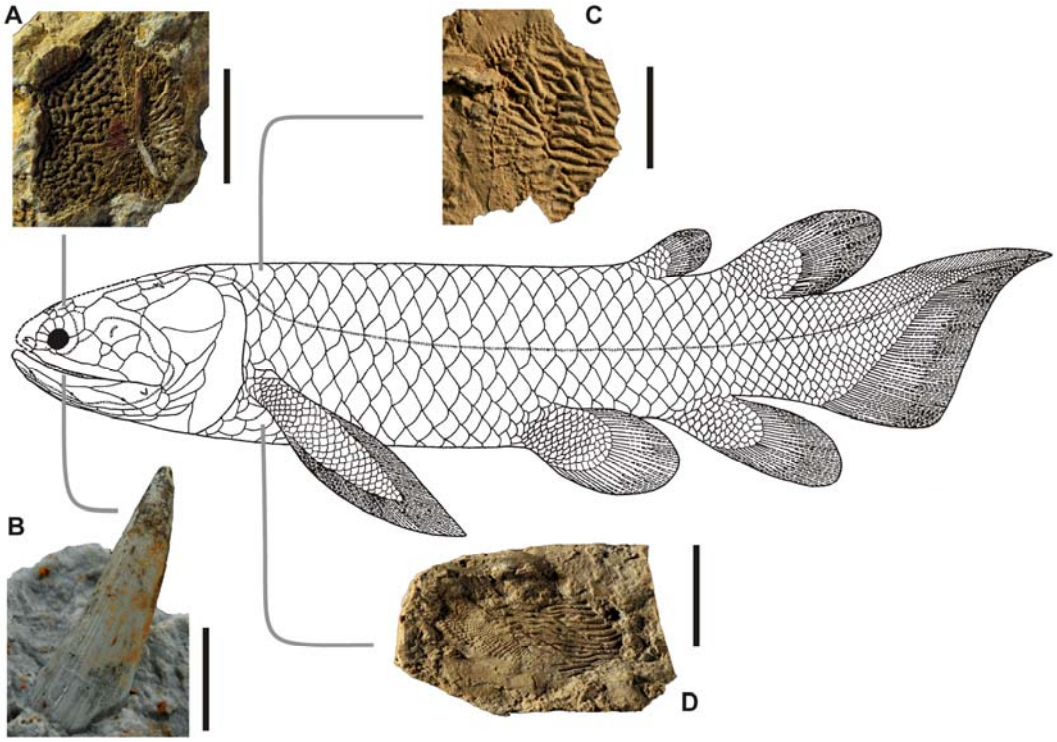


**FIGURE II.3. Specimens from the Cuche Formation (Frasnian) of Colombia attributed to an undetermined holoptychiid porolepiform** with their probable location on a reconstruction of *Holoptychius* from the Frasnian of Miguasha (Quebec). **A.** Parieto-intertemporal bone, **B.** Isolated fang, **C.** Isolated scale from the dorsal median row (reversed), **D.** Elongate isolated scale. Scale bar equals 1 cm. Completed and modified after CLOUTIER & SCHULTZE, 1996, and JANVIER & VILLARROEL, 1998.

In summary, this study has undisputedly confirmed the presence of holoptychiid porolepiforms in the Late Devonian of North-Western Gondwana, and enlarged the list of holoptychiid material from the Potrero Rincón fossil site of the Frasnian Cuche Formation (Fig. II.3). I am very eager to perform further fieldwork in the Devonian of Colombia in the future since the Colombian sites show the classic fish fauna that are normally associated with tetrapods in Euramerica (e.g., porolepiforms, rhizodontids, placoderms). The possibility of finding South American early tetrapods is extremely thrilling.

# Paper II

**A holoptychiid porolepiform (Sarcopterygii, Dipnomorpha) from the Frasnian of Colombia, with remarks on the Late Devonian Euramerica-Gondwana vertebrate faunal interchange.**

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**ABSTRACT**

The Late Devonian (Frasnian) fauna of the Cuche Formation of Colombia has provided important information on the taxonomical diversity and palaeobiogeographic relationships of the Late Devonian marginal marine vertebrate faunas of South America (North-western margin of Gondwana). Among this diverse vertebrate fauna, mostly composed of Gondwanan endemics, two reputedly Euramerican endemics have been found: the antiarchan placoderm *Asterolepis* and the porolepiform sarcopterygian *Holoptychius*. However, the occurrence of holoptychiid porolepiforms in the Frasnian of Colombia has been suggested based solely on the presence of 'holoptychiid-like' scales attributed to *Holoptychius*, although with caution. Here we describe further porolepiform remains that include a large isolated tooth with a typical dendrodont structure, additional '*Holoptychius*-like' scales, and a holoptychiid dermal cranial bone that bears sensory-line canals. These new finding provide clear evidence for the presence of holoptychiid porolepiforms in the Frasnian fauna of Colombia and suggest a possible brief Frasnian incursion of initially Euramerican vertebrate taxa into Gondwana, just before the massive Famennian expansion of several Gondwanan vertebrate taxa into Euramerica.

**Key words:** Devonian, Sarcopterygii, Gondwana, tooth histology, scales, paleobiogeography

## INTRODUCTION

The recent discoveries of the vertebrate fauna of the Cuche Formation of Colombia and of the Campo Chico Formation of Venezuela (Janvier & Villarroel, 1998, 2000; Young et al., 2000; Young & Moody, 2002) provided the first information about the diversity of the Late Devonian marginal marine vertebrate faunas of South America, thus of the westernmost Gondwana. Contrary to the previously known Devonian fish faunas of South America, which are essentially Lower Devonian in age and bound to deeper marine facies (Janvier & Maisey, 2010), these occurrences from Colombia and Venezuela are from siliciclastic, marginal marine to deltaic facies, and thus can be readily compared, as to their palaeo-environment, to a large number of more or less coeval vertebrate localities from Euramerica, Siberia, China and eastern or northeastern Gondwana. Therefore, they are important landmarks for reconstructing the palaeobiogeographic relationships of Devonian vertebrates during the period when the early tetrapods began to expand their distribution, and when Gondwana became closer and closer to Euramerica, thereby initiating the assembly of the Pangea.

The Venezuelan vertebrate fauna, was regarded as essentially composed of Gondwanan taxa known elsewhere from the Middle and Upper Devonian of Australia, Antarctica and South Africa (Young et al., 2000; Young & Moody, 2002), but the approximately coeval Colombian fauna (Janvier & Villarroel 1998, 2000; Janvier & Maisey, 2010) yielded, in addition to the same Gondwanan endemics, two taxa that have been tentatively referred to the antiarchan placoderm *Asterolepis* and the porolepiform sarcopterygian *Holoptychius*; that is, two reputedly Euramerican endemics. This finding suggested a possible brief Frasnian incursion of initially Euramerican vertebrate taxa into Gondwana, just before the massive Famennian expansion of several Gondwanan vertebrate taxa into western Euramerica (phyllolepids, groenlandaspids, rhizodontids, and possibly

megalichthyid tetrapodomorphs). This vertebrate faunal interchange probably had a considerable impact on the Euramerican coastal and lagoonal ecosystems by the end of the Devonian. However, although the Famennian expansion of Gondwanan vertebrate faunas into Euramerica becomes better and better documented thanks to increasingly detailed investigation in Famennian early tetrapod-bearing localities (Clément et al., 2004; Blieck et al., 2010), a passage of Euramerican taxa into Gondwana in about the same time still awaits confirmation.

Further field investigations in the Colombian Cuche Formation did not provide additional data that could unambiguously confirm the presence of *Asterolepis,* despite the remarkable resemblance between the isolated plates referred to this genus by Janvier and Villarroel (2000) and those of typical Euramerican *Asterolepis* species. Similarly, the occurrence of porolepiforms in the Cuche Formation has been inferred from the presence of 'holoptychiid-like' scales attributed to *Holoptychius*, although with caution (Janvier & Villarroel, 2000). However, the attribution of such isolated scale remains to *Holoptychius* is not a strong support for the presence of holoptychiids in the Frasnian of Colombia, due to the difficulty of identifying unambiguous apomorphies of this taxon based solely on isolated scale material (Cloutier & Schultze, 1996; Miller & Brazeau, 2007). New fossil evidence might confirm the occurrence of holoptychiid porolepiforms in the Late Devonian of Gondwana (Lelièvre et al., 1993; Johanson & Richie, 2000), provided that they clearly show diagnostic characters.

The Porolepiformes are an exclusively Devonian sarcopterygian taxon known from the early Lochkovian to the late Famennian that inhabited near-shore to possibly fresh water environments. They share a number of uniquely derived characters with living and fossil lungfishes and are therefore currently regarded as the sister group of dipnoans, within the Dipnomorpha (Ahlberg, 1991), although the inclusion of *Powichthys* in the Porolepiformes

raises questions on their phylogenetic position as an extinct stem dipnomorph clade, or a grade of early dipnomorphs (Schultze 2000; Friedman, 2007a,b). The order Porolepiformes comprises two families: the Porolepididae (a possible paraphyletic assemblage of primitive porolepiforms including *Porolepis* and *Heimenia*) (Ørvig, 1957, 1969; Clément, 2004) and the Holoptychiidae (comprising notably, *Holoptychius*, *Glyptolepis* and *Laccognathus*) (Jarvik, 1972; Ørvig, 1957; Cloutier & Ahlberg, 1996).

Nonetheless, all the species that are currently classified as Porolepiformes share at least one very conspicuous histological character, the dendrodont structure of their teeth (Schultze, 1969). In common with many early piscine sarcopterygians (formerly referred to as Rhipidistians), porolepiforms display a strongly folded structure of their teeth dentine. Schultze (1969, 1970) considered three main types of folded tooth structures, namely the dendrodont, polyplocodont and eusthenodont types, and regarded the dendrodont type as unique to the species that were, on the basis of other skeletal characters, gathered as Porolepiformes.

During the Early-Middle Devonian, the Porolepiformes display a change in scale morphology and microstructure (Ørvig, 1969; Schultze 1977, Mondéjar-Fernández & Clément, 2012) from small, rhombic, diamond-shaped scales covered with cosmine (a layer of dentine and enamel pervaded by a pore-canal system) in the “porolepidids”, to large, rounded scales that lose their cosmine covering and only retain a bony, vermiculate exposed surface prolonged anteriorly by an area covered with small, spoon-shaped dentine tubercles in the holoptychiids. The rise of the latter scale morphotype comes along with that of a similar type of ornamentation in the other dermal bones of the head and shoulder girdle that defines the clade Holoptychiidae, a group that became very abundant in marginal marine environments from the Late Emsian to the late Famennian in North America and Europe (Cloutier & Schultze, 1996; Schultze, 2000).

However, the ‘holoptychiid-like’ scale morphotype has proved to be very difficult to define, all the more that somewhat similar rounded scales occur independently in other sarcopterygian clades, notably onychodontids, actinistians and tetrapodomorphs (see Jarvik, 1980). Therefore, the record of holoptychiid scales in faunal lists is legitimately regarded as suspect by most early vertebrate specialists. So far, the only undoubted evidence for porolepiforms is the presence of dendrodont folded teeth.

Here we describe a large isolated -though poorly preserved- tooth whose typical dendrodont structure, along with ‘holoptychiid-like’ scales and a holoptychiid dermal cranial bone, provides clear evidence for the presence of holoptychiid porolepiforms, a reputedly Euramerican endemic taxon, in the Frasnian fauna of Colombia (North-western Gondwana).

**Institutional Abbreviations**

**MB**, Museum für Naturkunde, Leibniz Institute for Research on Evolution and Biodiversity at the Humboldt University, Berlin, Germany; **MNHN**, Muséum National d’Histoire Naturelle, Paris, France; **UN-DG-PALV,** Universidad Nacional de Colombia**,** Departamento de Geología, Colección de Paleontología (Vertebrados), Bogotá**,** Colombia.

## SYSTEMATIC PALAEONTOLOGY

Osteichthyes Huxley, 1880

Sarcopterygii Romer, 1955

Dipnomorpha Ahlberg, 1992

Porolepiformes Berg, 1937

Family Holoptychiidae Owen, 1860

Figs. 2 – 3a-b – 4 – 5

**Remarks:** Due to the incompleteness of the material and the difficulties to identify species or genera according exclusively to incompletely-preserved isolated bone remains or histological interpretations, we do not attempt to assign this material to any existing species or genus of holoptychiid.

## MATERIAL AND METHODS

The specimens described herein consist of an isolated tooth (UN-DG-PALV86), two partially preserved isolated scales (UN-DG-PALV50-51), and a skull roof dermal sensory canal bone (UN-DG-PALV87), found in the same layer as numerous isolated scales previously referred to as *Holoptychius* sp. by Janvier and Villarroel (2000); yet with reservation. All the material was collected by P. Janvier (MNHN, Paris) and C. Villaroel A (Prof. Emeritus at the Universidad Nacional de Colombia, Bogotá) in 2000 and 2004, and comes from the locality Potrero Rincón 3 of the upper part of the Cuche Formation (Department of Boyacá, Colombia) (Fig.1). The fossil remains occur in a channel within a thick series of reddish argillaceous sandstone, alongside numerous isolated *Bothriolepis* antiarch plates, and isolated dermal bones and teeth of various other fishes. Like all other vertebrate skeletal remains and the sediment from the same locality, the specimens are strongly weathered, because of the tropical climate (the weathering extending to about 30 cm below the surface). Nevertheless, the internal structure of the tooth is partly preserved in its basal portion, and two thin transverse sections were performed at two different heights after its inclusion in stratyl resin.

A series of casts of the scales were performed with elastomer resin stained in grey and brown and whitened with magnesium oxide before being photographed in the MNHN, Paris.

Comparisons with other holoptychiid fossil remains (teeth and scales of *Holoptychius* and *Laccognathus* from the MB, Berlin) were made. The thin sections were examined under natural transmitted and polarized light with a Zeiss Axiovert35 microscope. The specimens are deposited in the palaeontological collection of the Departamento de Geociencias of the Universidad Nacional de Colombia, Bogotá, Colombia.

**Geological context**

The Floresta Massif is located in the Central-North area of Colombia, in the Boyacá Department (Fig. 1a). It consists of a core of metamorphic rocks surrounded by Palaeozoic sediments. The Devonian there consists of three formations, from base to top: the El Tibet, Floresta and Cuche Formations (Fig.1b). The El Tibet Formation (Lochkovian?-Emsian) is made up by cross-bedded kaolinitic sandstone and virtually barren. The Floresta Formation (Emsian-Givetian/Frasnian) begins with a thick sandstone sequence and progressively passes to marine channel facies that yield rich invertebrate faunas and plants indicating Eifelian to possibly Frasnian ages for the latest (Berry et al., 2000). The Cuche Formation (probably all Frasnian) forms the top of the series (Fig. 1b). It consists of reddish sandstone, marls and clay lenses, and is uncomformably overlain by a Jurassic conglomerate. The Cuche Formation at the Potrero Rincón locality yields a rich vertebrate assemblage of acanthodians (*Nostolepis* sp., *Florestacanthus morenoi)* (Janvier & Villarroel, 2000; Burrow et al., 2003), chondrichthyans (*Antarctilamna* sp.?), placoderms (*Bothriolepis* sp., *Asterolepis* sp. and probably *Groenlandaspis* sp.), actinopterygians (Stegotrachelidae gen. et sp. indet.) and sarcopterygians (*Holoptychius* sp.?, Megalichthyidae gen. et sp. indet. and a rhizodontid erroneously referred to *Strepsodus* sp. ?) (Janvier & Villarroel, 1998, 2000; Jeffery, 2003, Burrow et al., 2003; Janvier & Maisey, 2010). This vertebrate fauna is associated with abundant plant remains (Berry et al., 2000), bivalves and lingulids, which suggest a low

energy marginal marine to brackish environment. This assemblage closely compares with that of the Givetian-Frasnian Campo Chico Formation of western Venezuela (Young & Moody, 2002), despite minor differences, such as the lack of lungfishes, phyllolepids and the asterolepidoid *Venezuelepis* in the Cuche Formation and the lack of *Asterolepis* and rhizodontids in the Campo Chico Formation. Nevertheless, in both formations, *Bothriolepis* is very abundant. The Colombian and Venezuelan occurrences are separated by about 500 km but belong to the same large Palaeozoic ensemble of the Central Cordillera that once referred to as the 'eastern Andean Terrane' (see Janvier & Villarroel, 2000; Young et al., 2000; Young & Moody, 2002, for further details).

## DESCRIPTION

### Tooth

**Overall morphology—**The tooth (UN-DG-PALV86) measures 2.1 cm in length (from the lowermost point of the exposed portion to the apex) and 0.7 cm in diameter at its base (Fig. 2a). It is slightly curved from the base to the apex. Although the tooth is isolated, it is most plausible that it was curved inwards (lingual curvature), a condition typical for piscine sarcopterygians and early tetrapods (Jarvik, 1972; Ahlberg and Clack, 1998). There is no presence of a reverse-curvature at the apex, a condition seen in rhizodontids (Jeffery, 2003), onychodontids (Andrews et al., 2006) and certain porolepiforms (*Hamodus* in Bystrow, 1939). The base of the tooth is not completely preserved, a very common condition for isolated teeth, so it is not possible to assert whether the tooth was also curved at its base or not. The presence of a bulked base cannot be confirmed either.

The external surface is gently striated by very thin, parallel striae. The striations extend continuously from the base to the apex, and are distributed along the entire surface of

the tooth. In the uppermost part of the apex the striae are more difficult to see, but they are still present. The striation pattern consists of both deep and more superficial plications, with one superficial thin stria generally located between two deep striae (Fig. 2b). There are around 20 deep striae, and accordingly, around another 20 superficial thin striae.

The tooth is rounded in cross-section, especially at its base, becoming slightly flattened towards the apex. However, no carina (or cutting edge) in the mesial and distal margins are present, contrary to the condition seen in the large teeth of holoptychiids like *Holoptychius*, *Laccognathus* or *Glyptolepis* (Bystrow, 1939; Jarvik, 1972). Due to its size, it can be described as a fang, although it is not possible to determine whether it was located in the upper or lower jaw.

**Histology—**The tooth has been greatly re-crystallized (re-mineralized) during fossilization. Osteo- and orthodentine have been replaced by mineral elements from the surrounding rock matrix and it is very difficult to identify the boundaries between them (Fig. 3a,b). However, the general branching pattern of the orthodentine matches closely the 'firelike' branching of the typical dendrodont plicidentine of porolepiforms (Fig. 3c,d). The pulp cavity was probably filled with osteodentine and it occupies about one-fourth (Fig. 3a) to one-half (Fig. 3b) of the inner surface of the tooth.

The inwards dentine folds are regular and numerous (around 40) and penetrate deeply towards the pulp cavity. Beneath the enamel layer and extending into the folds (i.e., globular zone, see Warren & Turner, 2006) the dentine tubules show a radiating pattern. The outer enamel rim has completely disappeared, however its thickness (around 10 μm) can be observed in certain regions as a hollow gap between the matrix and the dentine layer (Fig. 3a,b). The external plications seen on the external surface of the elastomer cast very likely match those of the missing enamel layer and are directly correlated to the dentine folds, as in

rhizodontids and ‘osteolepiforms’ (Jeffery, 2003). Because of the poor preservation issues and the weathering of the base of the tooth it is not possible to determine whether the bone of attachment penetrates between the dentine folds or not.

**Scales**

Two scales (UN-DG-PALV50, 51; Janvier & Villarroel, 2000) where chosen to illustrate the occurrence of ‘holotychiid-like’ scales in the Cuche Formation (Fig. 4). They are incompletely preserved due either to a fracture (Fig. 4a) or to an incomplete exposure (Fig. 4b). They measure up to 3 cm in length (approximatively), are rounded to elongate in shape, and devoid of cosmine. The external surface ornamentation consists of a series of spoon-shaped tubercles arranged in radiating rows, located mostly in the overlapped surface and extending posteriorly through the boundary between the overlapped and exposed surfaces. These tubercles prolong themselves posteriorly into the exposed surface and anostomose forming a series of antero-posteriorly elongate ridges that can vary in thickness.

Nevertheless because only the external surface of the scales is preserved it is impossible to observe the internal surface and to verify whether they possess an inner boss or not. The absence of internal surface ornamentation (i.e., articular ridges or bosses) in rounded, cosmine free scales occurs in holoptychiids, derived dipnoans, actinistians and onychodontids (Ørvig, 1957; Mondéjar-Fernández & Clément, 2012), whereas the presence of a wedge-shaped inner boss is characteristic of the convergently acquired rounded scales of tetrapodomorphs (such as rhizodontids and tristichopterid ‘osteolepiforms’) (Jarvik, 1980).

**Dermal, sensory line-bearing bone**

An isolated bone (UN-DG-PALV87) is preserved in two parts due to an internal fracture that splits the bone horizontally. The part described herein corresponds to the more

superficial one, visible in internal (ventral) view (Fig. 5a). The right and left margins are described as seen in Fig. 5. It is a dermal bone that bears a well-defined sensory canal running antero-posteriorly with a slight posterior curvature to the right. A series of smaller canals emerge from both sides of the main canal at the level of the posterior bend. The canal passes through the ossification centre of the bone, slightly postero-laterally displaced, and located at the level of the curvature of the main canal. The external contour of the bone is hexagonal, although its entire right margin is broken. The left margin is well preserved and shows two straight articulating facets. The natural cast of its dorsal, bony surface shows a vermiculate ornamentation.

According to the number, arrangement, and pattern of both the main and smaller secondary canals, and the angle of curvature of the main sensory canal, we identified this bone as a porolepiform left parieto-intertemporal bone ('fronto-dermosphenotic' *sensu* Jarvik, 1972, fig. 35). In porolepiforms, the parieto-intertemporal bone houses the junction between the supraorbital and infraorbital canals. The main canal can thus be considered as gathering the supraorbital canal (soc) (anteriorly) and the infraorbital canal (ioc) (laterally and posteriorly) (Fig. 5b). The well-preserved left margin of the specimen would correspond to the junction with the pineal plate (antero-laterally) and with the right parieto-intertemporal (laterally).

## DISCUSSION

### Tooth histology

The diversity of the tooth structure in vertebrates, and especially in sarcopterygians, has been well studied and documented since the pioneer works of Bystrow (1938, 1939). Bystrow's observations on the teeth of 'crossopterygians' were summarized and emphasized

by Schultze (1969, 1970). Schultze (1969) used the term plicidentine, first coined by Owen (1841), and then made formal by Tomes (1878), as ‘‘a tissue with true dentinal tubules, which is derived from the calcification of a pulp, the odontoblast-carrying surface of which has been rendered complicated by foldings of its surface’’ (Tomes in Warren & Turner, 2006:125). The structure and arrangement of the plicidentine has proven to be a key character for the study of tooth histological diversity in osteichthyans.

The presence of plicidentine around the pulp at the base of a tooth was considered a diagnostic feature of sarcopterygians crown to onychodontids and actinistians (Vorobyeva, 1977). However, folded dentine has also been described in the stem sarcopterygian Psarolepis from the Early Devonian of China (Yu, 1998; Zhu et al., 1999). Therefore, the presence of plicidentine can no longer be considered a synapomorphy of rhipidistians (Cloutier & Ahlberg, 1996) but would rather represent the primitive state for sarcopterygians.

Onychodontids and actinistians have simple, non-plicated teeth, which could be considered a secondary and probably convergent loss, whereas dipnomorphs and tetrapodomorphs show different dentine-folding morphotypes. Based on the degree and regularity of the dentine folding, Schultze (1969, 1970) identified three principal different plicidentine morphologies in rhipidistians: [1] Polyplocodont: the pulp cavity is free from osteodentine; the orthodentine is folded simply and irregularly with branches of first or second degree; and the bone of attachment extends between the folds (the labyrinthodont folding of early tetrapods is a variant of the polyplocodont one in which the branches of the folds are apparently lost and the bone of attachment does not penetrate into the folds); [2] Eusthenodont: the pulp cavity is filled with osteodentine; the orthodentine folding is often more complicated; and the bone of attachment extends between the folds as well; and [3] Dendrodont: the pulp cavity is filled with osteodentine, the orthodentine shows complicated

and regular folding (‘firelike’ branching); and the bone of attachment is restricted to the base of the tooth and does not extend between the folds.

Polyplocodont (present in some piscine sarcopterygians and in early tetrapods), labyrinthodont (present in several carboniferous tetrapods) and eusthenodont (present in ‘osteolepiformes’) foldings are merely phenetic descriptions of the overall form and structure of the plicidentine, and thus they cannot be considered autapomorphies of certain taxa; instead they are best regarded as organisational grades (Jeffery, 2003; Warren & Turner, 2006). However, dendrodont folding seems to be restricted to the Porolepiformes, and constitutes a well-established synapomorphy of the clade (Schultze, 1969; Panchen & Smithson, 1987). Vorobyeva (1977) cautioned that the dendrodont teeth could also have evolved in parallel among sarcopterygians, by analogy with the polyplocodont and eusthenodont teeth, as evidenced by the occurrence of plicidentine in *Psarolepis*. However, dendrodont plicidentine has not been found in any other sarcopterygian group so far; thus suggesting the validity of the dendrodont plicidentine as a distinguishable character of the Porolepiformes.

**Holoptychiid affinities of the specimens**

Our assignation of the specimens above described to the Holoptychiidae relies on both morphological and histological evidences. The simultaneous occurrence of such characters constitutes a strong evidence for the holoptychiid nature of these remains.

**Tooth**—The absence of an apex curvature clearly distinguishes our isolated tooth from the ‘rhizodontid-like’ teeth already described in the Cuche Formation (Janvier & Villarroel, 2000) and tentatively attributed to *Strepsodus* (but see Jeffery, 2003 for an alternative interpretation). Moreover in certain rhizodontid teeth where enamel folds occur, the striation pattern is different to that of our specimen. In *Rhizodus*, deep plications are restricted to the

base of the crown (Jeffery, 2003, fig.6), whereas in other rhizodontids like *Strepsodus* where striation spread across the entire surface of the crown, the striae do not follow the contour of the tooth, but are somewhat perpendicular to the attachment bone of the jaw (Jeffery, 2003, fig.11c-d). In our specimen the striae run parallel to each other and merge at the apex, following the contour of the tooth. This pattern is identical to that of porolepiforms like *Glyptolepis*, *Hamodus* or *Holoptychius* (Bystrow, 1939).

In porolepiforms, the size and degree of recurvature of the jaw teeth is variable, not only between parasymphysial teeth and coronoid fangs, but also among coronoid fangs, depending on their location in the jaw (Jarvik, 1972; Ahlberg, 1991, 1992a). In the lower jaw, the parasymphysial fangs are slightly recurved at their apex but do not exceed in height the coronoid fangs, except in the case of *Duffichthys* (Ahlberg, 1992a).

The absence of recurvature at the apex, the uniform striation pattern, and the absence of well-developed carinate margins are consistent with the condition seen in holoptychiid porolepiforms such as *Holoptychius*, *Glyptolepis* or *Hamodus* (Bystrow, 1939). However it differs from *Hamodus* in the absence of a hooked apex and sigmoid aspect. The absence of carinate margins is common in the teeth of several sarcopterygian groups (e.g., porolepiforms and ‘osteolepiforms’) and it is considered as another example of tooth morphological variability related to their position along the jaws, especially in the lower jaw (Jarvik, 1944, 1972; Ahlberg, 1992a).

When histology is considered, Schultze (1969, 1970) noticed that in the teeth of the primitive porolepiform *Porolepis* the osteodentine of the pulp cavity and the orthodentine are separated by a clear boundary. In holoptychiids both ortho and osteodentine grow closely connected, and no trace of a well delimited boundary between these tissues is visible. Such a boundary is not visible in any of our histological sections (Fig. 2), thus supporting its assignation to the Holoptychiidae. However, we should note that this boundary between

ortho- and osteodentine is also absent in the ‘porolepidid’ *Heimenia* from the Early-Middle Devonian of Spitsbergen (data not shown), thus adding a new feature suggesting the intermediate condition of *Heimenia* between *Porolepis* and the holoptychiids (Mondéjar-Fernández & Clément, 2012).

**Scales**— ‘Holoptychiid-like’ scale gross morphology is convergent with several other sarcopterygian groups (e.g., onychodontids, actinistians, rhizodontids, and tristichopterid ‘osteolepiforms’) and has proven to be a weak character for systematic assignment of isolated remains (see Ørvig, 1957). Moreover, the numerous species of *Holoptychius* have been mostly defined on the basis of disarticulated material and isolated scales (Cloutier & Schultze, 1996). The assignation of isolated scales to different species of *Holoptychius*, or even holoptychiids as a whole, can thus be considered suspect and poorly informative when such assignations rely exclusively on external descriptions of scale remains (Miller & Brazeau, 2007).

Nonetheless, the identification of isolated scale remains and their assignment to a certain sarcopterygian group must be based on a combination of as many key characters as possible, rather than on overall external morphology and ornamentation. Therefore, in the case of porolepiforms a valid holoptychiid synapomorphy is seen as the combined occurrence of [1] a rounded outline, [2] the absence of cosmine, [3] the presence of small spoon-shaped tubercles located in the posterior margin of the overlapped area and arranged in radiating rows, immediately preceding or extending into the exposed surface (although such spoon shaped tubercles may occur also in onychodontids), [4] the presence of antero-posterioly oriented ridges or blunt tubercles in the exposed surface, and [5] a smooth internal surface, without traces of bosses or articular ridges (Ørvig, 1957; Mondéjar-Fernández & Clément, 2012).

Among holoptychiids, systematic attribution of isolated scale remains to the different genera lies on very subtle differences in the ornamentation of the external surface. As described above, the external exposed surface of our scale material bears series of tubercles and bony ridges. The presence of such ridges has been identified in *Holoptychius*, *Quebecius* and *Glyptolepis* (Ørvig, 1957; Schultze & Arsenault, 1987; Cloutier & Schultze, 1996). The ridges in *Glyptolepis* and *Quebecius* are made of dentine and are narrower and more numerous than in *Holoptychius*. *Laccognathus* shows a unique ornamentation composed of rounded dentine tubercles or small ridges capped with enamel (Ørvig, 1957; Downs et al., 2011). The ridges of *Holoptychius* are solely made of bone and look thicker than in any other holoptychiid. However, their morphology is highly variable in different parts of the body (Ørvig, 1957); the scales of the ventral region can show stout bony tubercles arranged in rows alone, whereas dorsal and flanks scales show antero-posteriorly arranged bony ridges (Cloutier & Schultze, 1996). Nonetheless, among holotychiids, the combination of coarse bony ridges in the exposed surface associated with dentine spoon-shaped tubercles in the overlapped surface defines the genus *Holoptychius* and their occurrence in our isolated scale material justifies the previous attribution of these scales to *Holoptychius* sp. (Janvier & Villarroel, 2000).

**Parieto-intertemporal**—The dermal, sensory canal-bearing bone found along with the isolated tooth and scales described herein has been identified as a cosmine-free left parieto-intertemporal. Parieto-intertemporal bones are paired cranial roof bones covering the dorsal side of the braincase and are formed by fusion of the parietal and the intertemporal bones in porolepiforms, whereas in other sarcopterygians, such as *Eusthenopteron* the parietal and the intertemporal bones are present as separated elements (Jarvik, 1944). In ‘osteolepiforms’ the parietal bone (frontal *sensu* Jarvik, 1944) is elongated, whereas the intertemporal is narrow,

smaller than the parietal, and fits into the posterolateral corner of the latter. On the contrary the parieto-intertemporal bone of porolepiforms is rather square-shaped. Therefore, the stouter hexagonal shape of our specimen is closer to the porolepiform skull bone pattern. The extension of the parieto-intertemporal bone is variable among porolepiforms and, as proposed by Jarvik (1972), differences in proportion of the parieto-ethmoidal shield would enable to identify genera. However our specimen is isolated and no other cranial roof bones, isolated nor in connection, have been found in the Cuche Formation to allow comparisons.

The parieto-intertemporal bone bears a series of sensory canals. According to Jarvik (1972), the parieto-intertemporal is pierced by the supraorbital (soc), infraorbital (ioc), and prespiracular (prspc) canals (Fig. 5b). All these canals converge at the level of the radiation centre of the bone (Jarvik, 1972; fig.35a,b,d,e). The number, distribution and branching pattern of these canals are characteristic for porolepiforms; the sensory lines have been modified and their course displaced relative to that of ‘osteolepiforms’ in certain regions by the fusion or subdivision of several dermal cranial bones.

As described by Jarvik (1972) in the Porolepiformes the infraorbital canal (ioc) passes through the jugal and the postorbital, enters the parieto-ethmoidal shield and merges with the supraorbital canal (soc) at the centre of radiation of the parieto-intertemporal. At this place, the canal turns abruptly backwards and enters the postparietals. The prespiracular sensory canal (prspc) also converges in the parieto-intertemporal. However, this canal is absent from *Porolepis* and *Glyptolepis* but present in *Holotychius*. The prespiracular canal branches off from the infraorbital canal at the centre of radiation of the parieto-intertemporal and runs in a postero-lateral direction, more or less close to the infraorbital canal and to the postero-lateral corner of the parieto-ethmoidal shield, where it leaves the cranial roof and enters the prespiracular plate.

We were able to identify all these canals in our specimen (Fig.5b). However Jarvik noted that the insertion point, curvature, and number of minor canals are variable in dermal sensory canal bones, especially in porolepiforms (Jarvik, 1944, 1972). One of the small canals right to the main canal could correspond to the prespiracular canal (?pspc), diagnostic of *Holoptychius* among holoptychiids. However its presence cannot be confirmed with enough confidence due to the weathering of the right portion of the specimen. Therefore, we will limit our assignation of this dermal bone to an undetermined holoptychiid.

**Paleobiogeographic implications**

As Ahlberg (1992b) pointed out, our attempt to understand Devonian fish biogeography is rendered uneasy by the patchy distribution of data. Africa and South America still remain largely blank areas and they will most certainly reveal new taxa and unexpected biogeographical patterns in the years to come. Nonetheless our knowledge of vertebrate diversity during the Devonian in South America has been greatly improved in the last years by the discovery and thorough description of several Devonian fossil sites, from Venezuela and Colombia, to Brazil, Bolivia, and the Fakland islands (Janvier & Maisey, 2010).

The Eifelian-Frasnian vertebrate assemblages from Venezuela and Colombia are characterized by placoderm- and osteichthyan-dominated assemblages of the Devonian 'intertropical belt' (Janvier, 2007; Janvier & Maisey, 2010). The Floresta Formation and the overlying Cuche Formation (Upper Frasnian) of Colombia are considered to have been deposited under local shallow marine influence (Janvier & Villarroel, 1998, 2000). The depositional environment is considered as a low energy marginal marine to brackish waters, which is consistent with the classical environments associated with holoptychiid porolepiforms (Cloutier & Schultze, 1996).

The presence of a dendrodont teeth, *Holoptychius* sp. scales, and a porolepiform dermal bone in the Frasnian of Colombia confirms, beyond any doubt, the occurrence of holoptychiids in Gondwana before the Famennian. The presence of this typically Euramerican taxon in North-western Gondwana, together with the placoderm antiarch *Asterolepis*, also corroborates the migration of several Euramerican taxa to Gondwana prior to the posterior massive invasion of Gondwanan fish faunas to Euramerica during the Famennian (Janvier & Villarroel, 2000; Janvier, 2007; Janvier & Maisey, 2010).

The remaining question is in which way Euramerican taxa could have expanded their distribution into Gondwana during the Frasnian? Probable holoptychiid remains are known in the Middle Devonian of Iran (Frasnian) (Lelièvre et al., 1993) and the Late Devonian of Australia (Famennian) (Johanson & Ritchie, 2000) (Fig.6). It is thus difficult to conclude whether this expansion occurred through South America or through the Middle East, since both Colombian and Iranian faunas are almost contemporaneous. Nevertheless, our new data suggest that the vicinity of South-western Euramerica with North-western Gondwana could have been greater than previously suspected (see Young, 2003), which would have allowed fish faunas to disperse more easily from one continent to the other.

Another issue is what enabled northern faunas to migrate south earlier than the northward expansion of Gondwanan faunas; and why this 'exodus' seems to be restricted to antiarchs and porolepiforms? In the case of the Porolepiformes, and especially holoptychiids like *Holoptychius*, their more ubiquitous mode of life would have favoured their migration from North to South, probably through both eastern and western routes (Middle East and South America, respectively). Indeed 'porolepidids' are known from both marine and freshwater deposits from Euramerica, and recently from eastern Gondwana (Johanson et al., in press), whereas holoptychiids appear to have been somehow restricted to freshwater and possibly estuarine or lagoonal environments (Ahlberg, 1992b). However, both families are

widely distributed throughout the entire Devonian of Euramerica, thereby suggesting great adaptability and potential of dispersion of porolepiforms.

## CONCLUSION

This new discovery of undisputedly holoptychiid remains (*Holoptychius* sp.) in the Colombian Cuche Formation, combined with that of other Euramerican taxa such as the placoderm antiarch *Asterolepis* in the Upper Devonian of Colombia suggests that prior to the relatively now well-documented Famennian dispersion from Gondwana to Euramerica of endemic Gondwanan vertebrate taxa (such as phyllolepid and groenlandaspid placoderms, and rhizodontid and megalichthyid sarcopterygians) there was a limited incursion of Euramerican faunas into Gondwana by the end of the Frasnian (Janvier & Villarroel, 1998, 2000; Janvier, 2007; Janvier & Maisey, 2010).

As Janvier and Maisey (2010) pointed out, this Frasnian-Famennian interchange could have concerned exclusively fishes that were bound to marginal marine or fresh waters environments and, thus it would imply that South-western Euramerica and North-western Gondwana continental landmasses were contacting each other more closely than previously thought.

Holoptychiid remains (e.g., *Holoptychius*) are found in the vast majority of Devonian tetrapod localities of the world (Clément et al., 2004; Lebedev & Zakhrenko, 2010). The presence of *Holoptychius* sp. in the Frasnian of Colombia opens the possibility for the Cuche Formation to yield additional Late Devonian sarcopterygian fishes and possibly even early tetrapods.

Other vertebrate and sarcopterygian remains from the Devonian of South America await description. Further study and field work in the South American Devonian would

improve our knowledge on the environmental conditions associated with vertebrate faunas dispersion at the end of the Devonian and would shed more light on the paleobiogeographic relationships of South American to Gondwana and Euramerica during the Late Palaeozoic.

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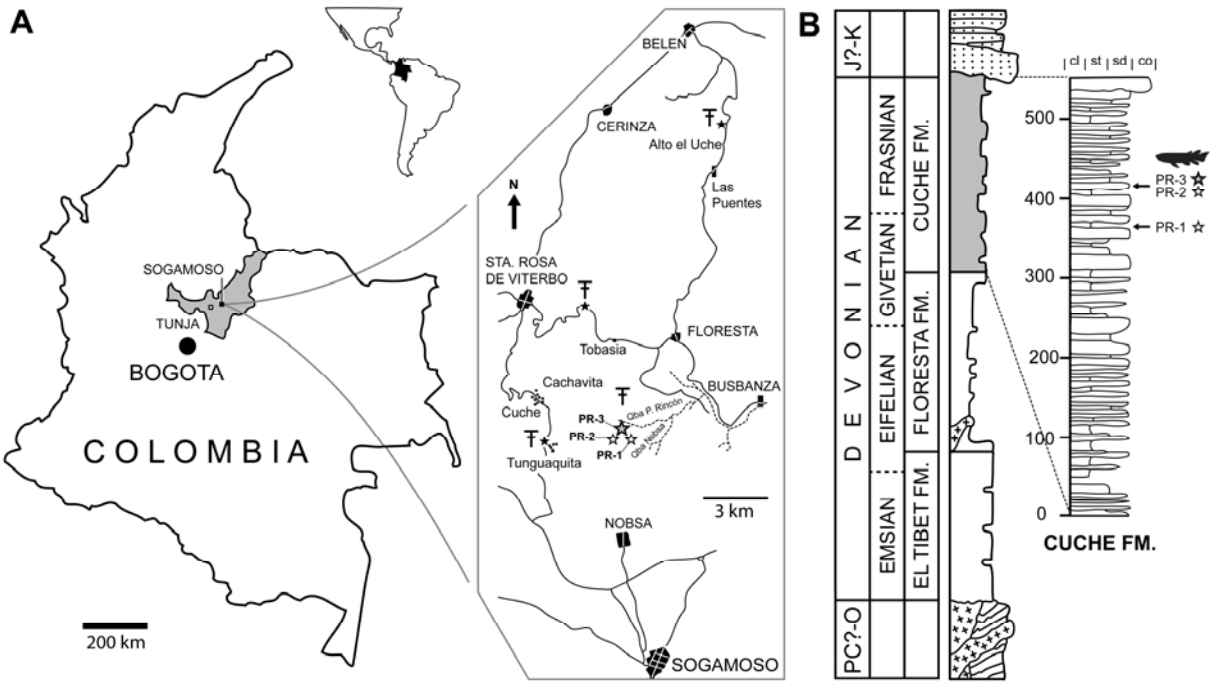
**FIGURE CAPTIONS**

**Figure 1**




**A.** Locality map of the Department of Boyacá (north-central Colombia). **B**. Synthetic log of the Cuche Formation, with special reference to the Potrero Rincón fossil sites (PR 1-3). White stars represent the Potrero Rincón fossil localities. Note that the holoptychiid porolepiform remains come from the PR-3 locality. Smaller black stars represent other fossil fish localities of the Boyacá department (see Janvier and Villarroel, 2000). **Abb**: **PC?-O,** Precambrian?-Ordovician, **J?-K**, Jurassic?-Cretaceous; **cl**, claystone; **st**, siltstone; **sd**, sandstone; **cg**, conglomerate. Modified and redrawn after Janvier and Villarroel, 2000.

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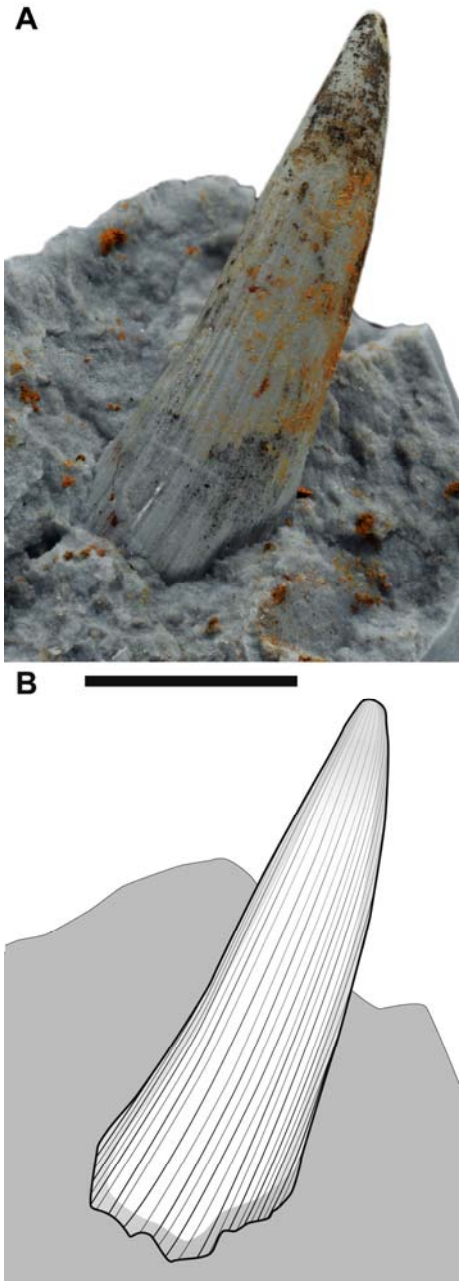
**Figure 2**




Isolated tooth of an undetermined holoptychiid porolepiform from the Frasnian of Colombia (UN-DG-PALV86). **A**. Elastomere cast of the specimen; **B**. Interpretative drawing. Scale bar equals 1 cm.

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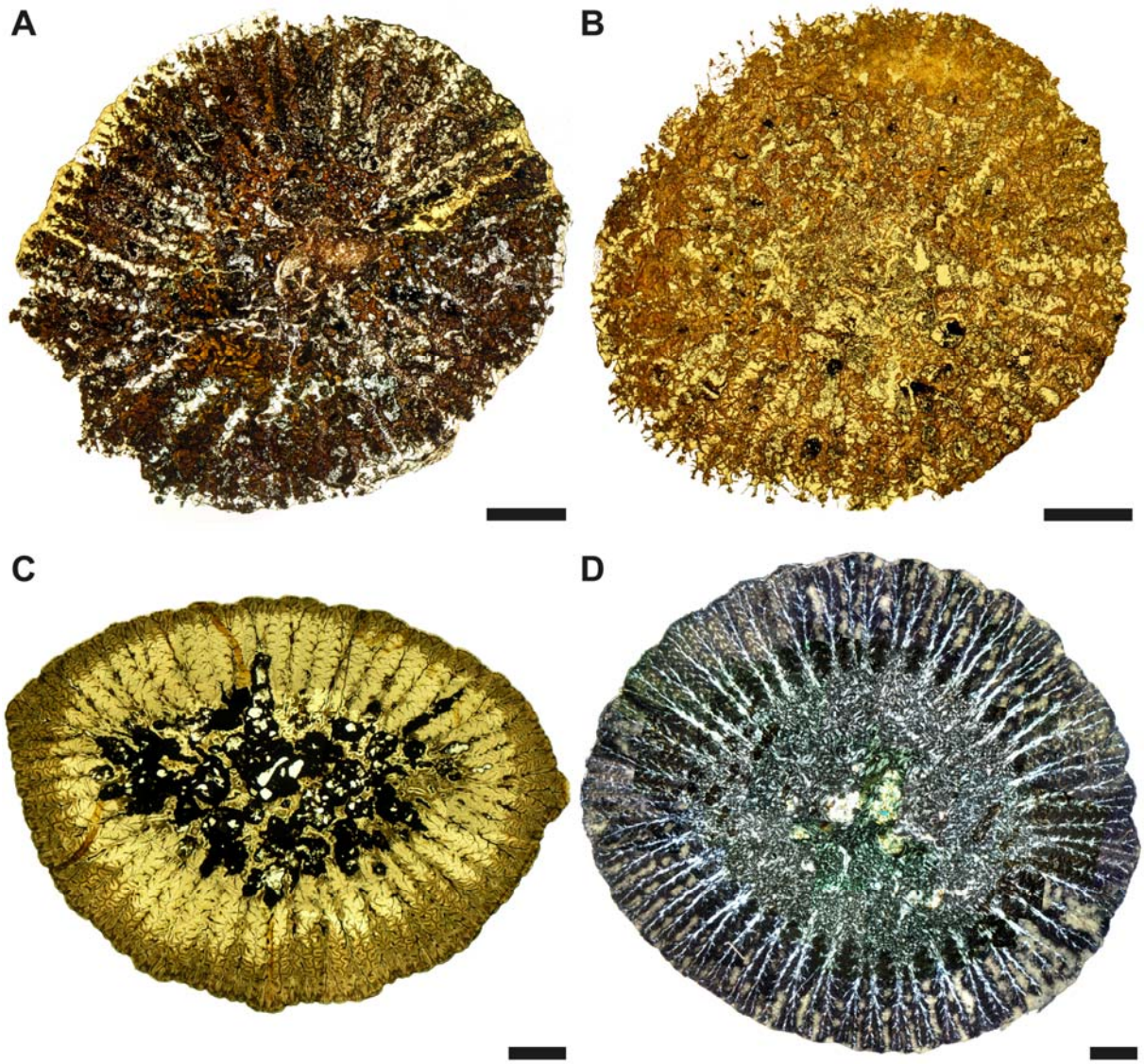
**Figure 3**




Cross sections of several holoptychiid porolepiform teeth. Note that all cross sections were made at approximately the same corresponding height at the base of the tooth. **A**. Undetermined holoptychiid from the Frasnian of Colombia (UN-DG-PALV86), lower cross section; **B**. Undetermined holoptychiid from the Frasnian of Colombia (UN-DG-PALV86), upper cross section; **C**. *Laccognathus* (MB.f. 1850) from the Givetian-Frasnian of Latvia; and **D**. *Holoptychius* (MB.f. 2129,4) from the Givetian-Frasnian of Latvia (in polarized light). Scale bar equals 1 mm.

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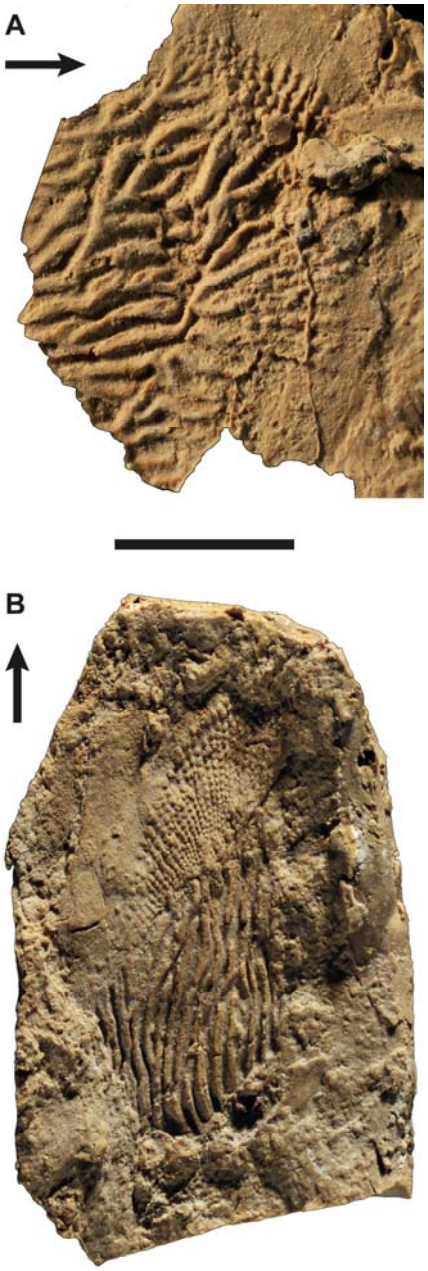
**Figure 4**




Elastomere cast of two isolated ‘holoptychiid-like’ scales (*Holoptychius* sp.) from the Frasnian of Colombia. **A**. Incompletely preserved isolated scale, probably belonging to the dorsal or flank region of the body (UN-DG-PALV50). **B**. Incompletely preserved isolated scale, slightly antero-posteriorly elongated, located probably near the base of a fin (UN-DG-PALV51). Arrows point anteriorly. Scale bar equals 1 cm.

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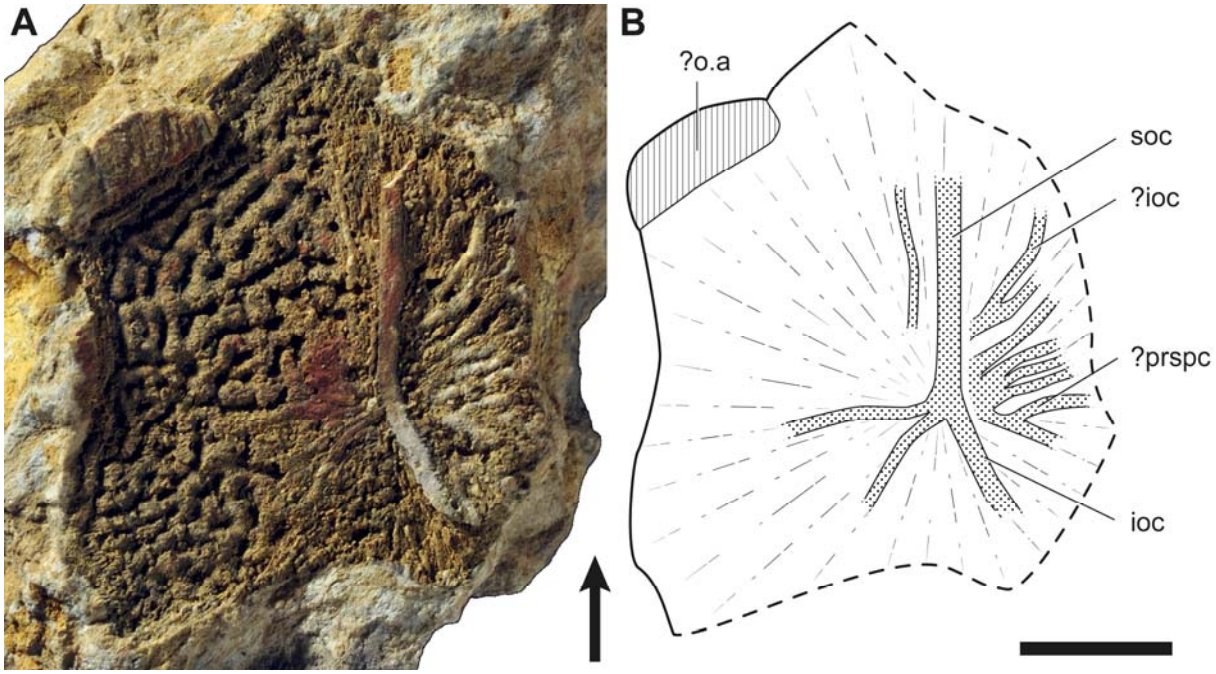
**Figure 5**




Left parieto-intertemporal bone of an undetermined holoptychiid porolepiform from the Frasnian of Colombia (UN-DG-PALV87). **A**. Specimen in ventral view; **B**. Drawing of the specimen in ventral view. **Abbreviations**: **ioc**, infraorbital canal; **?prspc**, prespiracular canal?; **?o.a,** overlapping area for the pineal plate?; **soc**, supraorbital canal. Arrow points anteriorly. Scale bar equal 50 mm.

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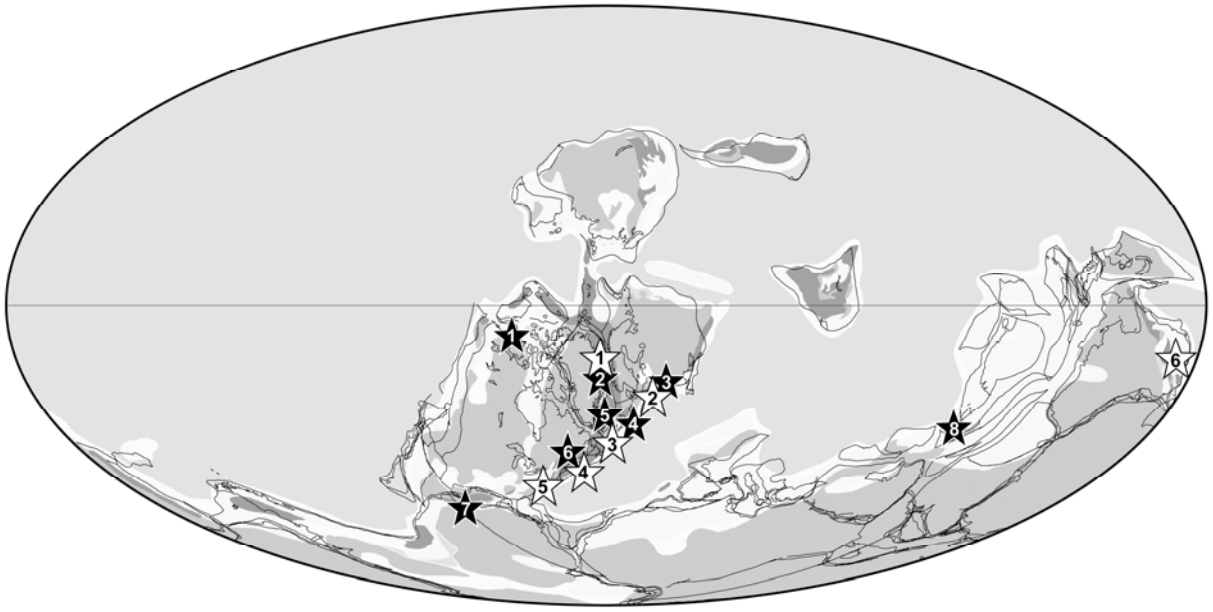
**Figure 6**



Palaeogeographical map for the Late Devonian illustrating the occurrence of holoptychiid porolepiforms in Euramerica and Gondwana. **Emsian-Frasnian localities** (black stars): 1. Arctic Canada (*Nasogaluakus, Laccognathus*) (Schultze, 2000; Downs et al., 2011); 2. East Greenland (*Holoptychius*, *Glyptolepis*) (Jarvik, 1972); 3. Russia and Latvia (*Holoptychius*, *Glyptolepis*, *Laccognathus*, *Hamodus*, *Paraglyptolepis*) (Obrutschew 1933; Vorobyeva, 1987); 4. Germany (*Glyptolepis*) (Gross, 1936); 5. Scotland (*Duffichthys, Holoptychius, Glyptolepis*) (Ahlberg, 1992); 6. Québec (*Holoptychius, Quebecius*) (Cloutier & Schultze, 1996); 7. Colombia (*Holoptychius* sp.) (Janvier & Villarroel, 2000; this study) ; 8. Iran (*Holoptychius*) (Lelièvre et al., 1993). **Famennian localities (white stars)**: 1. East Greenland (*Holoptychius*) (Jarvik, 1972); 2. Latvia (*Ventalepis*) (Schultze, 1980); 3. Belgium (*Holoptychius* sp.) (Clément et al., 2004); 4. Eastern Canada (*Holoptychius*) (Miller & Brazeau, 2008); 5. Pennsylvania (*Holoptychius, Glyptolepis*) ; 6. Australia (*Holoptychius* sp.) (Johanson & Ritchie, 2000). Redrawn and modified from Golonka, 2000 and Blakey, 2012. Planned for page width

## THE SCALES OF *TULERPETON CURTUM* AND THE DEVONIAN ORIGIN OF THE TETRAPOD SQUAMATION BAUPLAN

Amongst the three relatively well-known Devonian tetrapods, *Tulerpeton* is the least cited in comparison with *Ichthyostega* and *Acanthostega*, but it is certainly the most puzzling of them all (Fig. III.1) (LEBEDEV & CLACK, 1993). Although its postcranial anatomy is less well-represented than in *Ichthyostega* or *Acanthostega* and the shape of the caudal fin is still unknown, *Tulerpeton* possess a series of features on its limb skeleton that initially suggested its belonging to the crown group Tetrapoda, among the Reptiliomorpha (LEBEDEV & COATES, 1995). This derived position was challenged by AHLBERG and CLACK (1998) and currently, it is located among the stem Devonian tetrapods, crownward to *Acanthostega* and *Ichthyostega*, the three of them forming a series a 'successive' plesions along the Tetrapoda stem (CLOUTIER & AHLBERG, 1996; RUTA *et al.*, 2003; COATES *et al.*, 2008) (Chapter I, Fig. III.1.2).

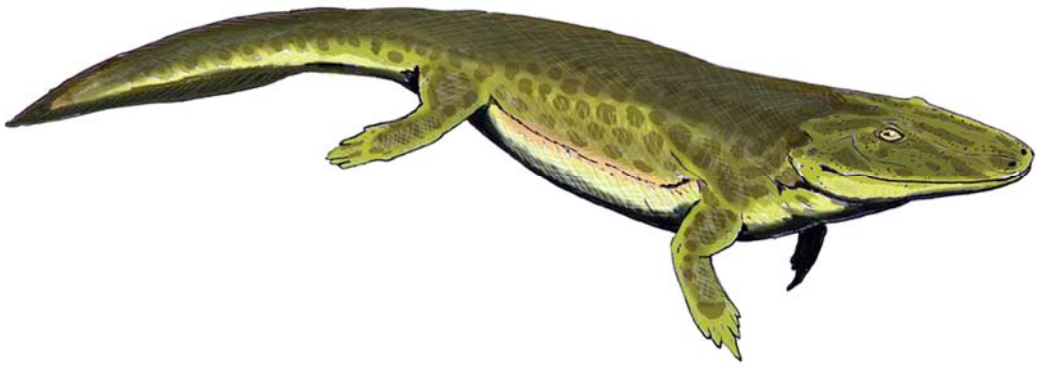


**FIGURE III.1. Artistic reconstruction of the Devonian tetrapod *Tulerpeton curtum*.** © Wikimedia Commons.

The squamation of *Tulerpeton* is, together with that of *Acanthostega*, the best and most completely preserved of all Devonian tetrapods. The scales are scattered all around the holotype block, with numerous scales disarticulated and/or in connexion (Fig. III.2). The great number of scale remains offers the opportunity to investigate crucial aspects of their arrangement, morphology and microstructure under a diverse set of techniques without damaging the other elements of the holotype. This study of the scales of *Tulerpeton* thus represents the first thorough morphological and histological analysis of the dermal scales of a Devonian tetrapod.

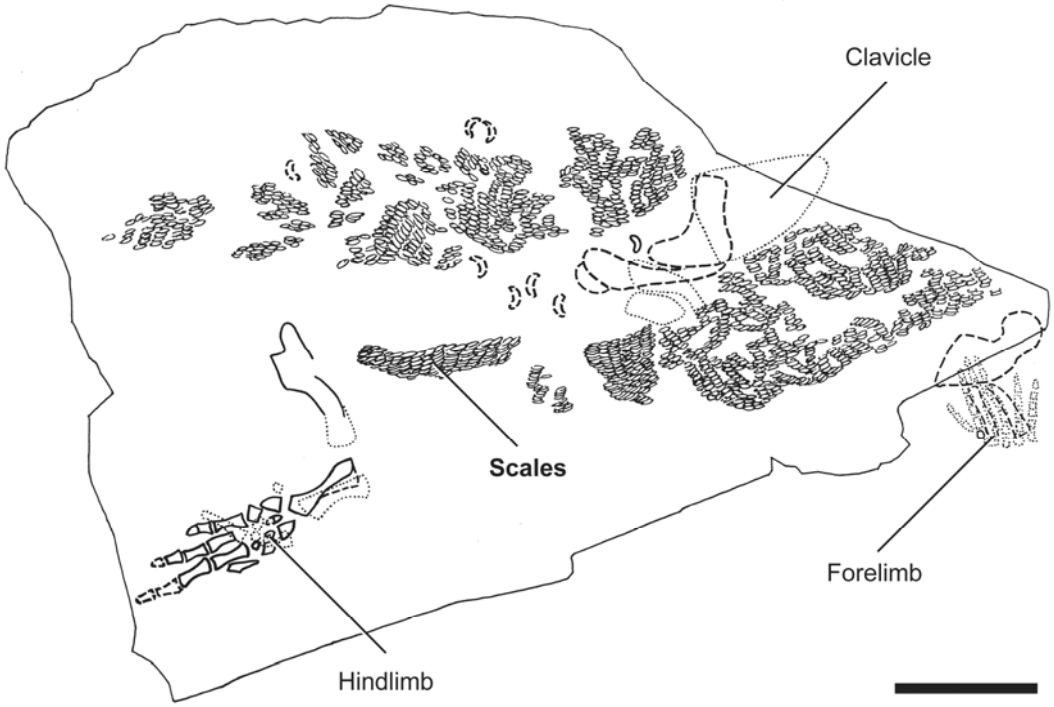



**FIGURE III.2. *Tulerpeton curtum,* holotype (PIN 2921:7).** Diagram showing the distribution of the specimens in a block of matrix. Bones indicated by solid outlines are exposed at the level of horizontal cleavage through the block, coinciding with the extensively preserved scale cover. Dashed outlines indicate material found above this level, and dotted outlines indicate material found beneath. All the bones have now been removed and prepared. Scale bar equals 50 mm. Modified after LEBEDEV & COATES, 1995.

When Gaël CLÉMENT went to North-western Russia from 2009 to 2011 for field survey on Devonian localities he brought back, with the permission of Oleg LEBEDEV, several small scale-containing matrix blocks from the holotype of *Tulerpeton curtum* from the PIN of Moscow. He passed them onto Sophie SANCHEZ who scanned them in the ESRF of Grenoble. I finally got the data on the summer of 2010 and started the virtual reconstruction in the '3D platform' of the MNHN of Paris. I worked on two data sets: a general acquisition of a scale-containing block (5,05 µm of voxel size) and a close-up from the same block (0.678 µm of voxel size). The synchrotron data were astonishing in image quality and contrast between the scale remains and the surrounding matrix.

The segmentation process under Mimics was long. Segmentation was manual in all slices (1800 slices, 5,05 µm voxel size; 1600 slices, 0.678 µm voxel size) and each slice was individually corrected from segmentation imprecisions (Chapter II, Fig. II.2.3.1). Despite all these time-consuming operations, the virtual work furnished great results, notably the entire reconstruction of a complete isolated scale and an inset of the same scale from which I could extract certain histological information.

Although I had already finished the virtual treatment, I wanted to investigate further the nature of the bone tissue in the scales. That is why I decided to perform two cross sections on scale from the holotype material of *Tulerpeton*. The histological cross-sections might seem redundant now that I had scanned and reconstructed the scales, but the synchrotron data, despite their extraordinary quality, were unable to reveal the presence of Sharpey's fibres and processes of bone growth. In the end, both sources of data were complementary and, when put together, they delivered a much more detailed and concise picture of the scales of *Tulerpeton* (Fig. III.3).

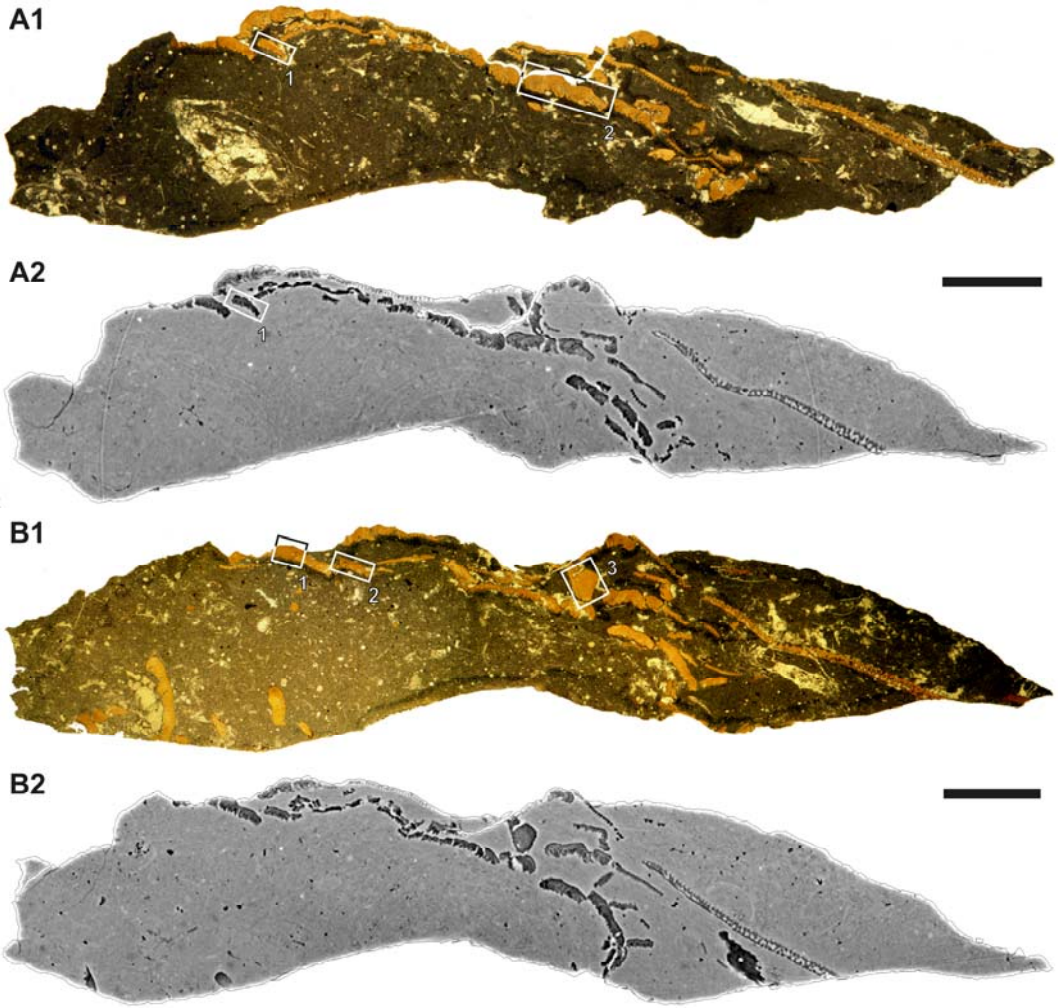



**FIGURE III.3. Comparison between 'classic' palaeohistological and synchrotron light cross sections in a scale containing block of *Tulerpeton curtum*** (PIN 2921/3238). The synchrotron microtomographic slices (**A2**, **B2**) were chosen to match the histological ground sections as close as possible (**A1**, **B1**). Squared insets are detailed in higher magnification in Figure 2 of Paper III. Scale bar equals 100 µm.

The virtual reconstruction (Paper III, fig. 1) shows an elongate ovoid scale, similar to that figured by LEBEDEV and COATES (1995, fig. 14). This scale morphotype is the most commonly found in the large holotype block (Fig. III.2) along with small rounded scales covering the limbs. However, a closer look at the scales from the small block points to the recognition of minute spindle-shaped scales in *Tulerpeton*, a scale

morphotype known in *Acanthostega* (COATES, 1996) and inferred in *Ichthyostega* (CLACK, in DAESCHLER *et al.*, 2009). However, I could not confirm the occurrence of spindle-shaped scales in *Tulerpeton* based solely on the scratchy material at hand. Further comparison with the holotype block and other scale remains from the PIN might confirm my initial suppositions.

Comparing the morphology and histology of *Tulerpeton*'s scales with that of other sarcopterygian fishes made me realize that the interpretation of early tetrapod's squamation and the plesiomorphic morphotype from which the tetrapod scale derives is highly dependent on a stable and well-resolved phylogenetic framework that supports the recognition of homologous structures and evolutionary patterns. However, recent histological descriptions of key taxa (e.g., *Eusthenopteron, Panderichthys*, and *Tiktaalik*) (ZYLBERBERG *et al.*, 2010; WITZMANN, 2011; RICHTER *et al.*, 2011) and new phylogenetic studies on tetrapodomorph interrelationships (COATES & FRIEDMAN, 2010; SWARTZ, 2012) have raised some doubts on certain hypothesis of tetrapodomorph interrelationships. Moreover, the discovery of new tetrapodomorph taxa, like the putative stem "elpistostegalian" *Tinirau* (SWARTZ, 2012), and the restudy of uncertainly placed "osteolepiforms", like *Litoptychus* (COATES & FRIEDMAN, 2010), *Platycephalichthys* (VOROBYEVA, 1962, 1977b), and *Glyptopomus* (JARVIK, 1950), urge to look more closely at the morphological disparity of the derived "osteolepiform" stock and their common features, convergent or not, with tetrapods.

Finally, it has been said that the postcranial and appendicular skeleton give to *Tulerpeton* the appearance of a more terrestrially adapted animal (LEBEDEV & COATES, 1995). Although mainly aquatic, *Tulerpeton* might have relied more on air for breathing than water because gill-supporting structures have not been found (LEBEDEV & COATES, 1995) and therefore it has been stated that it probably lacked internal gills (LONG &

GORDON, 2004). The results of Paper III point to the histological similarity between the scales of *Tulerpeton* and those of terrestrial Carboniferous tetrapods (WITZMANN, 2011). Moreover, *Tulerpeton* may represent an off-shot from the 'classical' evolutionary scenario proposed for early tetrapods, which states that tetrapods evolved in shallow, freshwater environments, crowded with plant remains similar to the extant mangrove environments (CLACK, 2002a). This globally accepted scenario was challenged by the discovery of the Middle Devonian tetrapod trackways from Poland (NIEDZWIEDZKI *et al.*, 2010) that were produced during a low tidal phase of a marine environment. *Tulerpeton* remains were recovered from sediments representatives of a warm and shallow marine-influenced estuarine paleoenvironment (LEBEDEV & COATES, 1995). This coastal marine habitat thus approaches the 'primitive' condition of the putative earliest tetrapods as suggested in NIEDZWIEDZKI *et al.* (2010) and raises many questions on the environments where tetrapods initially appeared. Future work should reconsider the timing, ecology and environmental setting of the fish–tetrapod transition, and more particularly define whether the first tetrapods were primitively fresh water or marine animals and to what extent the were able to cope with differences in salinity.

# Paper III

**The scales of *Tulerpeton curtum* and the Devonian origin of the tetrapod squamation Bauplan**

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**ABSTRACT**

Certain aspects of the early stages of the evolution of tetrapods (limbed vertebrates) are still incompletely known, especially those concerning the modifications of the dermal skeleton. The skin and the associated dermal ossifications of early tetrapods are key structures involved in fundamental aspects of their metabolism, way of life and locomotion. Early tetrapods were extensively covered with dermal scales, inherited from their lobe-finned fish relatives. The transition to land (or terrestrialization) of tetrapods during the Late Devonian and Carboniferous are thought to have produced important changes in the squamation modifying scale size, shape, overlapping pattern, and histological microstructure of the scales. However, the evolutionary implications of such changes are still largely unexplored, mainly due to the lack of comparative data. *Tulerpeton curtum* from the Late Devonian of Russia is one of the earliest representatives of the limbed vertebrates and one of the rare Devonian tetrapods known in substantial anatomical detail. The good preservation of the enabled to study several aspects of scale morphology and microstructure. The use of high-resolution synchrotron microtomography allowed performing the first highly detailed three-dimensional reconstruction of the scales of a Devonian tetrapod. The new data show that the scales of *Tulerpeton* share the same bone-tissue characteristics as those of younger tetrapods. The differences between 'tetrapod-like' scales and 'fish-like' sarcopterygian scales probably arose rapidly in tetrapods during the Devonian in an aquatic environment. These new histological and morphological features were maintained and almost unmodified during the terrestrialization and subsequent evolution of tetrapods during the Carboniferous.

**Key words**: histology; synchrotron microtomography; early tetrapods; scale evolution; terrestrialization

## INTRODUCTION

Among the multiple morphological changes that took place during the so-called 'fish-tetrapod transition', those concerning the evolutionary modifications of the integumentary dermal skeleton have received little attention in recent descriptive publications of new taxa (e.g., Jarvik, 1996; Coates, 1996; Clack and Finney, 2005; Daeschler et al., 2006). Nonetheless the skin and the associated dermal ossifications of vertebrates, and more particularly of tetrapods are key structures determining several fundamental aspects of their metabolism, way of life and locomotion (e.g., Castanet et al., 2003; Witzmann, 2007, 2011).

The tetrapod dermal skeleton comprises a variety of osseous structures such as ornamented flat bones and tooth-bearing bones, the teeth themselves, cementing tissues (e.g.,'bone of attachment'), and the diverse mineralized products of the skin, including scutes, shields, scales, and osteoderms (see Vickaryous and Sire, 2009 for a revision).

Most Palaeozoic tetrapods were extensively covered with ossified, overlapping dermal scales, similar in many respects to those of osteichthyans in general, and sarcopterygian fishes in particular (Romer, 1956; Janvier, 1996). The transition to land (or terrestrialization) of tetrapods during the Late Devonian and Carboniferous (Clack, 2002; Steyer, 2012) is thought to have affected the squamation in every possible way modifying scale size, shape, overlapping pattern, structure and thickness of the different histological layers, and the bone-tissue nature of the scales (see Witzmann, 2011 for a thorough revision). Dermal scales were lost in several tetrapod groups during the Late Paleozoic and Mesozoic, and replaced by osteoderms as the main integumentary mineralized structures (Vickaryous and Sire, 2009).

A key evolutionary modification related to scale morphology in sarcopterygians (lobe-finned fishes) concerns the transition from a primitive thick rhombic morphotype with a cosmine covering (i.e., a combination of odontogenic tissues unknown in extant vertebrates in

which the enamel and dentine layers are pervaded by a complex pore-canal system) to a derived thin rounded morphotype devoid of cosmine during the Devonian. This transition is known to have occurred independently in dipnoans (Schultze, 1969), porolepiforms (Ørvig, 1957; Mondéjar-Fernández & Clément, 2012), and "osteolepiforms" (Jarvik, 1985). Interestingly, a similar scenario may have occurred between "elpistostegalians" (such as *Elpistostege*, *Panderichthys* or *Tiktaalik*), with rhombic scales devoid of cosmine (Vorobyeva and Schultze, 1991; Schultze, 1996; Daeschler et al., 2006), and Devonian tetrapods (such as *Ichthyostega*, *Acanthostega*, and *Tulerpeton*) with rounded, ovoid, or spindle-shaped scales (Jarvik, 1996; Coates, 1996; Lebedev and Coates, 1995).

Devonian and Carboniferous tetrapods present a wider range of scale morphotypes than sarcopterygian fishes and certain show a secondary recovery of a 'squared' morphotype (rhombic *sensu* von Meyer, 1858; Witzmann, 2007, 2011), different from the plesiomorphic rhombic morphotype of their fish relatives. Moreover, early tetrapods, and especially Devonian ones, are characterized by a combination of derived characters (e.g., the presence of digits, a specialized otic region, etc.) and plesiomorphic features (e.g., retention of gills and a fin rays-supporting tail, etc.) (Clack, 2002). The morphological and histological characteristics of the scales place the squamation among the derived characters associated with the origin of tetrapods (Clack, 2002; Witzmann, 2011). However, comparative data are lacking in most Devonian tetrapods and more precise descriptions are needed to confirm or refute past observations and to suggest evolutionary morphological scenarios.

*Tulerpeton curtum* from the Late Devonian (Famennian) of Russia (Lebedev, 1984) is one of the earliest representatives of the limbed vertebrates and, along with its contemporaneous *Ichthyostega* and *Acanthostega* from East Greenland, one of the rare Devonian tetrapods known in substantial anatomical detail. Among the well-preserved and diverse postcranial material (Lebedev and Coates, 1995), the squamation is represented by

numerous isolated scales, some of them are still in connection. Their number and their good preservation state enable to study several aspects of their distribution and arrangement along the body, morphological diversity between different scale morphotypes, and microstructure.

Two scale morphotypes have been observed in *Tulerpeton*: 1) ovoid scales, probably covering the complete surface of the trunk; and 2) smaller, rounded scales located on the limbs (Lebedev and Coates, 1995; Witzmann, 2007, 2011). Witzmann (2007) proposed that in *Tulerpeton* the scales of the ventral region were most likely arranged in an en-chevron pattern, as in *Acanthostega* and other Carboniferous tetrapods. However this configuration cannot be confirmed in the holotype due to postmortem multiple folding of the skin (Lebedev and Coates, 1995). Scales located on the belly of early tetrapods have been called gastral scales rather than 'gastralia', in order to avoid confusion with the gastralia or 'abdominal ribs' present in several amniotes (Romer, 1956; Claessens, 2004; Vickaryous and Hall, 2008; Witzmann, 2007, 2011). Herein we will refer to these scales, when present in Devonian tetrapods, as ventral scales in order to facilitate comparisons with the ventral scales of sarcopterygian fishes.

The use of high-resolution synchrotron microtomography allowed performing the first highly detailed three-dimensional reconstruction of the scales of a Devonian tetrapod. The visualization of the inner microstructure and the outer ornamentation of both sides of a *Tulerpeton* scale provides new and important comparative information on the histological structure and morphological evolution of the squamation in early tetrapods.

**Institutional Abbreviations**

**ESRF**, European Synchrotron Radiation Facility, Grenoble, France; **MNHN**, Muséum national d'Histoire naturelle, Paris, France; **PIN**, Palaeontological Institute of the Academy of Sciences of Russia, Moscow, Russia.

## MATERIAL AND METHODS

### Material

The early tetrapod *Tulerpeton curtum* Lebedev 1984 comes from the Late Devonian (Famennian) deposits of the Andreyevka locality, Tula region (Central Russia). Most of the postcranial material belongs to the holotype (PIN 2921/7), which consists of a partial skeleton from a single individual comprising complete and articulated right fore and hindlimbs in which the digits are preserved (Lebedev and Coates, 1995). With the exception of the holotype, other tetrapod remains (especially skull bones) have been found in the Andreyevka locality but they cannot be definitely assigned to *Tulerpeton curtum* (Lebedev and Clack, 2003) thus suggesting the occurrence of more than one species of tetrapod in the Tula region. All tetrapod remains from the Andreyevka locality were recovered from sediments of a warm and shallow marine-influenced estuarine paleoenvironment (Lebedev and Coates, 1995).

The scales herein studied (PIN 2921/3238 and PIN 2921/3239) come from the large matrix block including the holotype of *Tulerpeton curtum* (PIN 2921/7) (see Lebedev and Coates, 1995, fig. 2), and confirm that our observations deal precisely with *Tulerpeton curtum* Lebedev 1984. The large amount of isolated scales dispersed in the holotype block allows performing histological ground sections in this otherwise unique material. All the fossil specimens are housed at the PIN (Moscow).

### Methods

The scale samples from the holotype consisting on two small matrix blocks containing numerous scales (PIN 2921/3238 and PIN 2921/3239), were studied by means of different methods. 1) Different scales were imaged using phase-contrast synchrotron microtomography at the ESRF, at the beamline ID19 (Sanchez et al., in press; Tafforeau and Smith, 2008): PIN

2921/3238 was imaged according to a multiscale approach (from a voxel size of 5.05µm to 0.678µm) and PIN 2921/3239 was imaged with a voxel size of 0.678. The series of high-resolution scans provided the basis for a virtual three-dimensional reconstruction of a scale from PIN 2921/3238 with the software Mimics (version 14.0) at the MNHN (Paris). The medium resolution (5.05µm) scan was done with a FreLoN 2K14 CCD camera (fast readout low noise) coupled to a Gadolinium oxysulfide 5µm thick scintillator. The scan was made in half acquisition using pink beam. The machine mode was in 7/8 multibunch. The beam was filtered with 0.25mm of tungsten, 0.25mm of copper and 2mm of aluminium. The gaps of the undulators U32 were opened to 60, thereby leading to a energy close to 60keV (Sanchez et al., in press). The time of exposure was of 0.2s. The sample was imaged with 5000 projections over 360° in a continuous mode. The sample was placed at 800mm from the detector. High-resolution scans (voxel size of 0.678µm) were performed using a single crystal 2.5nm period W/B4C multilayer Monochromator, a Gadolinium Gallium Garnet crystal 10µm thick scintillator and a FreLoN E2V CCD camera. The experiment was performed at 52keV. The beam was filtered with 1mm of aluminium and 0.25mm of copper. The machine mode was in 16 bunch. The scan was performed with 2000 projections over 180° in a continuous mode. The time of exposure was of 1.5s. The samples were fixed at 150mm from the detector. Data were reconstructed with a phase retrieval approach (Paganin et al., 2002). 2) Traditional techniques were also used to complete the microtomographic observations. The outer ornamentation was studied by means of SEM visualization at the PIN (Moscow) in scales from the holotype block (PIN 2921/7). 3) Complementary histological cross sections were performed in one of the scale-containing blocks (PIN 2921/3238) at the MNHN (Paris). The block was embedded in stratyl resin and sectioned in order to obtain a section of a thickness of approximately 25–30 µm. The final sections were examined under natural transmitted and polarized light with a Zeiss Axiovert35 microscope.

## DESCRIPTION

**External morphology**—The gross morphology of the modelled scale from PIN 2921/3238 specimen (Fig. 1 D,E) matches in many respects with the original description of Lebedev and Coates (1995), but differs in others. The restored scale measures up to 9 mm long and 4 mm wide. It is subelliptical, anteroposteriorly elongated with both anterior and posterior rounded margins, thus corresponding to the ovoid morphotype. The scale has a global convex external surface and a concave internal surface. The central part of the external surface is convex and is surrounded by a wide oval area that is concave in most cases; whereas the outer rim is again convex.

Towards the central (mesial) region, the scale is extremely thin, and shows a rather homogenous thickness throughout its length. The scale has been crushed and microfractured during fossilization resulting in the collapse of its mesial part along the antero-posterior axis thus attesting of the extreme thinness of this region. The lateral margins are thickened and recurved inwards resembling the handles of a plate in external view. The left anterior margin (as in Fig.1 D) is swollen more prominently than the opposing one, sometimes significantly and shows a straight fold that breaks the general symmetrical and rounded outline of the anterior portion. This condition is not restricted to the modelled scale but also occurs in other large ovoid scales of the holotype block (see supplementary information) and may be linked to the position of the scale on the right or left flank on the body. Comparisons with other scales preserved *in situ* in the holotype suggest that the modelled scale is a right flank scale.

The 3D model shows that the surface, which we considered as external (see the discussion below), can be divided into two well-defined portions relying on their ornamentation: a smooth (unornamented) large anterior overlapped area; and a vermiculated (ornamented) reduced posterior exposed area. The exposed ornamented area comprises the

posterior third of the scale length and shows a series of randomly distributed osseous tubercles, more pronounced anteriorly, near the limit between the overlapped and exposed areas. No clear longitudinal bony ridges as described by Lebedev and Coates (1995) have been identified in the modelled scale due to the incomplete preservation of its posterior margin. However, the presence of several longitudinal bony thickenings in the posterior most tip of the scale could correspond to the ridges described and figured by Lebedev and Coates (1995, fig. 14). Nevertheless, new observations on the holotype block suggest that it is possible that scales of different parts of the body could differ in their ornamentation (see discussion).

The surface of the scale that we consider internal is not entirely smooth as previously thought (Lebedev and Coates, 1995). The 3D model and the SEM pictures show that it is extensively covered by a series of small ridges, distributed in radial rows, orthogonally arranged to the concentric growth rings, and aligned with the growth axis of the scale, thus conferring to this surface the appearance of a wrinkled paper sheet (Fig. 1 E). The SEM images show that these ridges are formed by minute osseous tubercles that are aligned like beads and rest on a surface made of lamellar parallel osseous fibres (Fig. 1 F,G,H,I). No keel or articular ridge has been identified. The centre of ossification, well visible in the posterior region of the internal surface, is smooth, rounded, and concave. This region, representing the first stages of growth of the scale, can thus be defined as the ‘proto-scale’ and is surrounded by well-defined small concentric growth lines.

Large concentric and antero-posteriorly elongate growth rings (i.e., LAGs, lines of arrested growth) are clearly seen on both surfaces of the scale. Between five and seven equidistant growth rings are visible, following a series of regularly spaced concentric cracks that presumably match episodes of arrested growth (Fig. 1 D,E).

**Scale microstructure—**Microtomographic data and histological thin sections enable to reconstruct the inner structure of the scales (Fig. 2). The scales are solely made of compact, cellular bone. The bone tissue is composed of parallel-fibered bone (Fig. 2 A-E). Osteocyte lacunae of slightly variable size (10 μm wide and up to 100 μm long approximately) are clearly visible, especially in the thickened lateral margins (Fig. 2 A). The 3D model shows that the osteocytes embedded into the bone are elongate along the antero-posterior axis of the scale (Fig. 2 D). They are arranged in parallel and densely distributed along the scale thickness, especially next to what we consider to be the internal surface margin of the scale (Fig. 2 B).

No vascular canals have been identified; the bone can thus be considered as avascular. There are no traces of bone remodelling. A few rare, thin Sharpey's fibres have been identified with polarized light (Fig. 2 E1, E2). Growth marks are visible in the thickened edges as marginal circumferential waves parallel to the lateral scale margins (Fig. 2 A). The basal isopedine layer (i.e., a basal layer of lamellar bone formed by a plywood-like structure of the collagen fibers), characteristic of the scales of sarcopterygian fishes, is missing in *Tulerpeton*.

## DISCUSSION

### Scale Morphology and Ornamentation

Early tetrapods retained a well-developed scale covering along the whole body inherited from their lobe-finned relatives (Colbert, 1955; Romer, 1956; Janvier, 1996). However, regionalization of the squamation is more marked in tetrapods than in other sarcopterygians (e.g., dipnoans, actinistians), which show a rather homogenously distributed set of similarly-shaped scales. The differentiation of flank and ventral scales is a feature of

tetrapodomorphs (i.e., all taxa more closely related to tetrapods than to lungfishes) (Ahlberg, 1991), with the possible exception of rhizodontids (Andrews, 1985) and tristichopterids (Jarvik, 1980) with rounded scales. The squamation of rhombic-scaled tetrapodomorphs is divided in two main different scale regions: a dorsal/flank region of oblique, posteroventrally oriented scale rows; and a ventral (gastral) region of oblique, posterodorsally oriented scale rows. The ventral and dorsal oblique scale rows meet at an angle of approximately 90º along a line of 'inversion scales', which represents the 'ventrolateral ridge' separating both regions (Jarvik, 1948). However, in tetrapodomorph fishes, dorsal and ventral scales do not differ significantly in shape and/or ornamentation (e.g., "osteolepiforms" and "elpistostegalians"). The only differences are of size, the ventral scales being slightly smaller than the dorsal ones (J.M.F. pers. obs). This is not the case for tetrapods in which differences between dorsal and ventral scales affect size, shape, and ornamentation altogether (Witzmann, 2011).

In early tetrapods the dorsal scales are less heavily ossified than the ventral scales, and this fact could explain that they are not often preserved in fossil specimens, especially in Devonian forms (Jarvik, 1996; Coates, 1996). When preserved, dorsal scales are thin, often rounded to oval in shape, and show well defined growth rings (e.g., in temnospondyls) (Witzmann, 2007). Moreover, in certain derived groups, such as stereospondylomorphs, dorsal scales are closely arranged together but they no longer overlap each other (Janvier, 1992; Witzmann, 2007; Maganuco et al., 2009). Eventually dorsal and flanks scales disappeared in tetrapods, whereas the ventral scales were maintained.

Ventral scales may be of different morphotypes: rounded, ovoid, spindle-shaped, or secondary 'squared', the latter being the most frequent in Carboniferous tetrapods (Wiztmann, 2007). These morphotypes are not mutually exclusive and certain temnospondyls (e.g., *Sclerocephalus*, *Archegosaurus*) can present them at the same time or at different ontogenetic stages (Witzmann, 2007). Moreover, morphological transitions between each morphotype are

possible. The ‘squared’ morphotype can also be found dorsally in certain Carboniferous tetrapods such as colosteids (Witzmann, 2011).

Among Devonian tetrapods in which squamation is preserved, *Acanthostega* has spindle-shaped ventral scales arranged in an en-chevron pattern (Coates, 1996) and presents the same telescoping pattern as in temnospondyls (Witzmann, 2011). *Ichthyostega* possess small rounded scales located on the hindlimbs and tail (Jarvik, 1952, 1980), and recently J. Clack (*in* Daeschler et al., 2009) identified a few isolated comma-shaped ventral scales in cross sections on East Greenland specimens that correspond to the spindle-shaped morphotype. *Tulerpeton* presents only two of the four known scale morphotypes: small rounded scales in the limbs resembling those on the tail of *Ichthyostega* (Jarvik, 1952); and ovoid scales in the trunk similar to those of the dorsal region of *Greererpeton* (Godfrey, 1989) (Fig. X). No spindle-shaped scales similar to those of *Acanthostega* (Coates, 1996) have been identified with confidence in *Tulerpeton*. Moreover, ‘squared’ scales, similar to those of temnospondyls (Wtzmann, 2007, 2011) are not known in *Tulerpeton* or in any other Devonian tetrapod. Their occurrence seems to be restricted to post Devonian tetrapods (see below).

In *Tulerpeton* the degree of overlapping of the ovoid scales is extensive (the overlapped region extends more than up to 50% of the scale total length), as previously described by Lebedev and Coates (1995). A regular degree of scale overlapping is plesiomorphic for the rhombic scales of osteichthyans in general (Gemballa and Bartsch, 2002) and rhombic and rounded sarcopterygian fishes in particular, except in dipnoans and actinistians, which rounded scales show great overlapped portions, especially in extant forms (e.g., *Neoceratodus, Latimeria*) (Millot and Anthony, 1958; Burdak, 1979; Pridmore and Barwick, 1993). Transition from ancestral rhombic scales to derived rounded scales usually concerns mostly the overlapped region and is probably related to its morphofunctional importance in locomotion (e.g., Burdak, 1979; Mondéjar-Fernández and Clément, 2012). Our

new data on *Tulerpeton* show that the overlapped area of the scales undergoes a stronger positive allometric growth along the antero-posterior axis relative to the exposed area. The ovoid and extensively overlapping scales of *Tulerpeton* would represent another convergent character of early tetrapods with extant dipnoans and actinistians (e.g., *Neoceratodus, Latimeria*) (see Coates, 1994).

Large overlapped regions of the scales in sarcopterygians are smooth (e.g., dipnoans) or may sometimes show a crescent ornamentation of dentine or osseous tubercles located in the limit between the overlapped and exposed areas (e.g., onychodontids, actinistians, and holoptychiid porolepiforms). Such tubercles are absent in the overlapped region of *Tulerpeton* scales, which is smooth and unornamented, as in rhizodontids, "osteolepiforms", and "elpistostegalians" (Jarvik, 1980; Vorobyeva and Schultze, 1991; Daeschler et al., 2006). Moreover, the presence of what appears to be a series of large and well-marked osseous tubercles in the exposed region of the external surface of the scales in *Tulerpeton* (Fig. X A) is reminiscent of the condition seen in *Panderichthys* (Witzmann, 2011, fig.1,2), *Tiktaalik* (Richter et al., 2011), and *Glyptopomus* (Jarvik, 1950).

**Histology**

The scales of tetrapods show a structural simplification when compared with those of other sarcopterygian fishes. "Fish-like" scales of sarcopterygians are composed of two distinctive regions: 1) a superficial layer that can be formed by the outer cosmine layer and the cancellous underlying bony layer, and 2) a basal layer (isopedine) that can be associated with a bony zone made of woven-fibered bone forming the keel of the rhombic scales. The tetrapod scale Bauplan differs from this plesiomorphic condition; the separation in superficial and basal layers is no longer present; the scales are solely made of compact bone and the basal layer (isopedine) and odontogenic cell products (i.e., enamel and dentine layers) disappeared

completely (Witzmann, 2011). The loss of odontogenic components is convergent in several sarcopterygian fishes (e.g., several holoptychiids, derived dipnoans, rhizodontids) and constitutes one of the synapomorphies of the clade formed by the tristichopterids, "elpistostegalians", and tetrapods (clade Eotetrapodiformes *sensu* Coates and Friedman, 2010). Such modifications could be related to a reduction of weight of the dermal skeleton, limiting visceral compression and increasing the trunk flexibility (Witzmann, 2011).

Among tetrapodomorph sarcopterygians, the histological structure of *Tulerpeton* scales is more similar to that of *Eusthenopteron* and *Panderichthys* scales than to other cosmine-covered "osteolepiforms". The superficial layer of the scales of *Eusthenopteron* is made of poorly-vascularised parallel fibered bone in their outer part and vascularised woven-fibered bone in the core of the scales (Zylberberg et al., 2010). The scales of *Panderichthys* are also made of paralled-fibered bone in the outer region but the core of the scale is highly vascularised appearing thus as cancellous (Witzmann, 2011). However both *Eusthenopteron* and *Pandericthys* retain a basal isopedine layer. Among tetrapods, *Tulerpeton* scales resemble those of the Triassic temnospondyls *Plagiosuchus* and *Gerrothorax* (Stereospondyl Plagiosaurids) (Witzmann, 2011), which also show a single layer of compact, cellular bone tissue with numerous elongate osteocyte lacunae.

In *Tulerpeton* the osteocyte lacunae are numerous in the thickened margins and near the ornamented internal surface (Fig. 2 A,B). Moreover, the bone deposit between each line of arrested growth is thicker in the visceral portion of the scale (Fig. 2 A) than in the outer portion. Bone is deposited centrifugally from the core of the scale outwards as successive growth 'waves' parallel to the edges of the scale. This condition constitutes a strong argument to support our interpretation of this ornamented surface as the visceral or internal side of the scale (Castanet et al., 2003).

Osseous remodelling is considered as a characteristic of the tetrapod scales (Francillon-Vieillot et al., 1990; Castanet et al., 2003). Among tetrapodomorphs, bone remodelling is known in the scales of "osteolepiforms" (e.g., *Osteolepis, Megalichthys and Eusthenopteron*) (Gross, 1956; Zylberberg et al., 2010), but is not that developed in "elpistostegalians" such as *Panderichthys* and *Tiktaalik* (Witzmann, 2011; Richter et al., 2011). Its presence in *Acanthostega* and *Ichthyostega* cannot be confirmed due to the lack of histological data. However the scales of temnospondyls and other Carboniferous tetrapods have been thoroughly studied (Witzmann, 2011 and references therein) and show a relatively frequent bone remodelling. Our data show that osseous remodelling does not occur in the *Tulerpeton*'s scales probably due to the lack of vascular canals in the core of the scale. In turn, the absence of vascular canals could be related to the extreme thinness of the scales for which an important blood supply via internal vascular canals would not be needed.

The isopedine layer is missing in *Tulerpeton*. This condition is shared by all post Devonian tetrapods (Witzmann, 2011). Astonishingly, the internal surface ornamentation of the *Tulerpeton* scales is strongly reminiscent of the exposed middle layer (spongiosa) of other sarcopterygian scales (e.g., porolepiforms, rhizodontids, and "osteolepiforms") when the isopedine layer was broken during fossilization (see Jarvik, 1948, fig. 6 and pl. 37). Moreover, rounded scales devoid of cosmine (e.g., tristichopterids and rhizodontids, Jarvik, 1980) often show a series of radial striations in the anterior region of their internal surface (J.M.F., pers. obs). These striations become more visible when the thickness of the basal isopedine layer decreases and are more evident in thin rounded scales than in the well-ossified rhombic scales of basal cosmine-covered "osteolepiforms" and "elpistostegalians" (Jarvik, 1980; Witzmann, 2011). Recently, Zylberberg et al. (2010, fig.2 C2) showed in *Eusthenopteron* cross sections that the contact surface between the woven-fibered bone forming the lower part of superficial layer and the underlying basal layer is not straight;

instead the bone shows little indentations that penetrate the isopedine. These indentations can be reasonably associated with the radial striations observed in the rounded scales of tetrapodomorphs as previously described.

Thus, in *Tulerpeton*, the presence of an ornamented margin well visible throughout the internal surface of the scale could be due to: 1) a complete disappearance of the isopedine layer; or 2) an unmineralized isopedine layer that remained in a collagenous state and hence was not preserved in the fossil specimens. This last condition will lead to the exposure of the parallel-fibered bone tissue at the contact surface between the superficial and the basal layers. We prefer the latter scenario since partial to completely lack of mineralization of the basal layer is a common feature of the so-called elasmoid scales of several actinopterygians teleosts (Sire and Meunier, 1981), extant sarcopterygians (e.g., *Latimeria* and *Neoceratodus*) (Castanet et al., 1975; Meunier, 1984), and of the lissamphibian gymnophionans (Zylberberg and Wake, 1990). Moreover, the absence of Sharpey's fibres, reflecting the absence of a relationship between the ornamented internal surface and surrounding soft tissues is consistent with the non-preservation of an unmineralized basal layer is consistent with the non-preservation of an unmineralized basal layer. The strange ornamentation of the internal surface of the *Tulerpeton* scales could therefore correspond to the inferior margin of the superficial layer made of parallel-fibered bone that become apparent when the collagenous basal layer was not preserved during fossilization. A collagenous basal layer could thus represent the first stage towards the complete disappearance of the isopedine in tetrapods during the Carboniferous.

**Ontogenetic Status of the *Tulerpeton* Holotype**

Our 3D model and other *in situ* scales from the holotype block show between five and seven lines of arrested growth (LAGs or growth rings) on both surfaces (Fig. 1). Growth rings

are usually deposited annually in tetrapods (Castanet et al, 1993). Therefore, in *Tulerpeton* we see at least six growth episodes, corresponding to at least six Devonian years (Kahn and Pompea, 1978). Moreover, the space between two successive LAGs is generally equal (around 500 μm) along the entire surface of the scale. It implies that there was no clear deceleration in growth rate, which would have been recorded by more closely spaced LAGs towards the outer margins (Ombredane and Bagliniere, 1992). This would suggest that even if the holotype of *Tulerpeton* had possibly entered adulthood, it had not reached the plateau characteristic of fully-grown adults (Sanchez et al., 2008).

**Evolutionary Considerations and Implications**

Scale morphology has been generally neglected as a strong phylogenetic feature of sarcopterygian interrelationships due to its inherent convergent properties (Mondéjar-Fernández and Clément, 2012). Nevertheless histological structures may play a new and important role in heated phylogenetic debates such as tetrapodomorph interrelationships (i.e., all taxa more closely related to tetrapods than to lungfishes) (Ahlberg, 1991). Recent histological descriptions of key taxa (e.g., *Eusthenopteron, Panderichthys*, and *Tiktaalik*) (Zylberberg et al., 2010; Wiztmann, 2011; Richter et al., 2011) and new phylogenetic studies (Coates and Friedman, 2010; Swartz, 2012) have raised some doubts on certain straightforward hypothesis of tetrapodomorph interrelationships. Histological characters of the squamation may furnish new and interesting comparative elements (Fig. 3).

New data and thorough phylogenetic studies on “osteolepiform” and “elpistostegalian” interrelationships are needed, and the puzzling combination of features (e.g., rhombic scales lacking cosmine) present in uncertainly placed “osteolepiforms”, like *Platycephalichthys* (Vorobyeva, 1962, 1977) and *Glyptopomus* (Jarvik, 1950), urge to look more closely at the morphological disparity of the squamation of derived tetrapodomorphs and their common

features, convergent or not, with tetrapods. Such new studies would help to better assess the interpretation of early tetrapod's squamation and to establish more precisely the plesiomorphic morphotype from which the tetrapod scale derives.

The current phylogenetic pattern of squamation evolution states that it is more parsimonious (and certainly more probable) that rounded or ovoid scales as those of tristichopterids and tetrapods derive from a primitive rhombic morphotype as the one present in cosmine covered "osteolepiforms" and "elpistostegalians". Witzmann (2011) established an evolutionary scenario for the transition from the rhombic "elpistostegalian" scale to the 'squared' tetrapod scale, but only for the ventral scales. However, because the squamation evolution affected all kinds of scales in different parts of the body, then following this scenario, dorsal rounded to ovoid scales in tetrapods must also derive from the ancestral rhombic scales of "elpistostegalians", not just the 'squared' ventral ones. Unfortunately, Witzmann's scenario (2011) is over simplistic and does not take into account the loss of the basal layer in Carboniferous tetrapods when he homologizes the internal keel of "elpistostegalians" with the anterodorsally oriented crest of the tetrapod 'squared' scale. Indeed, the disappearance of the bony keel in tetrapods always follows the loss of the basal isopedine layer, but not the other way around. Examples of transition from rhombic to rounded scales where the isopedine layer is maintained (e.g., holoptychiids, tristichopterids, rhizodontids) show that the internal keel can be modified or disappear completely despite the maintenance of the isopedine layer (Mondéjar-Fernandez and Clément, 2012). However, it seems that in tetrapods the loss of the isopedine layer carries the loss of the keel.

As above described, no 'squared' ventral scales have been observed in Devonian tetrapods. If ventral (gastral) scales are considered to have evolved in tetrapods as a protection of the viscera from compressions while the animal was resting or lying on the ground (R. Holmes *in* Witzmann, 2011), then well ossified, secondary 'squared' ventral scales are

unlikely to be found in Devonian tetrapods, which were mainly aquatic, shallow water dwellers, and could hardly left the water (e.g., Clack, 2002). 'Squared' scales of Carboniferous tetrapods reduce trunk flexibility and, at the same time, enhance thrust production by a flexible tail (Witzmann, 2007), the result being an improvement of the acceleration stroke during locomotion (as in crocodiles) (Frey and Salisbury, 2001). Therefore, the telescoping spindle-shaped ventral scales of *Acanthostega,* and possibly *Ichthyostega*, are consistent with a greater trunk flexibility related to a more horizontally sinusoidal model of swimming associated with a well-developed "fish-like" caudal fin. The 'squared' scales of Carboniferous tetrapods would then represent a secondary acquisition of a rectangular outline from an ovoid or rounded morphotype present in Devonian tetrapods.

Witzmann (2007) proposed an ontogenetic and phylogenetic scenario for the squamation evolution in temnospondyls. Based on a well-preserved and complete ontogenetic series of the Carboniferous-Permian temnospondyl *Sclerocephalus*, Witzmann (2007) associated three well-defined morphotypes of the ventral scales to three ontogenetic stages. Rounded to ovoid scales correspond to a "larval" morphotype, spindle-shaped scales correspond to the "juvenile" morphotype, and 'squared' scales correspond to "adult" morphotype. However it is difficult to test such ontogenetic trends in Devonian tetrapods, mainly due to the absence of ontogenetic series for those forms. Following this scenario, Witzmann (2011) proposed that the ovoid shape of the *Tulerpeton* scales could represent a retained larval stage.

The rounded to ovoid scale morphotype of tetrapods (as evidenced in *Ichthyostega* and *Tulerpeton*) was present in the earliest ontogenetic stages in the flanks and ventral region, and was slightly modified in the ventral region into the spindle-shaped morphotype in more advanced ontogenetic stages (as in *Acanthostega* and possibly in *Ichthyostega*). A secondary 'squared' morphotype may have evolved afterwards during the Carboniferous and spread

throughout the ventral region from the spindle-shaped morphotype, as confirmed by ontogenetic series of temnospondyls (Wiztmann, 2007). The 3D model confirms that the ovoid scales of *Tulerpeton* are externally convex and internally concave, with well-defined thickened margins recurved inwards. This condition resembles the ventrolateral ovoid scales of temnospondyls such as *Archegosaurus* and *Sclerocephalus* (Witzmann 2007) that also develop spindle-shaped ventral scales during their ontogeny. Thus, as Witzmann (2007) proposed, the ventral (gastral) scales of Carboniferous/Permian tetrapods, whether they are ovoid, spindle-shaped or secondary 'squared', can be traced back from a simpler rounded to ovoid morphotype, similar to that of *Tulerpeton*.

## CONCLUSION

New methods and observations on the scales of *Tulerpeton* revealed a series of new characters related to the growth mode, biology, and evolutionary relationships of this early tetrapod and constitute a new referential amount of histological information on our knowledge of the evolution of the squamation in sarcopterygian tetrapodomorphs at the end of the Devonian.

The new data on *Tulerpeton* have modified the former orientation of the scales proposed by Lebedev and Coates (1995) and suggest that the overlapped external surface was smooth, whereas the exposed area was ornamented with osseous tubercles similar to those of "elpistostegalians". The internal surface shows a smooth and well-defined rounded ossification centre from which spreads an array of radial ridges formed by beads of minute osseous tubercles corresponding to the irregular internal margin of the exposed superficial bony layer. The basal layer (isopedine) is absent; it was probably unmineralized. The strange

ornamentation of the internal surface of the fossil scales would thus correspond to the exposed inferior margin of the bony superficial layer.

Histological observations have shown that the ovoid scales of *Tulerpeton* and the 'squared' scales of Carboniferous tetrapods share the same bone-tissue characteristics, with the exception that in the thick, adult scales of certain temnospondyls bone remodelling is more important. Thus, ovoid and 'squared' scales would belong to the same ontogenetic series, and as Witzmann (2007) proposed the ventral scales of all post-Devonian tetrapods, whether they are ovoid, spindle-shaped or secondary 'squared', can be traced back, ontogenetically and phylogenetically, from a simpler rounded to ovoid morphotype, similar to that of *Tulerpeton*.

The differences between the derived 'tetrapod-like' scale condition (i.e., scales solely made of compact bone and lacking enamel, dentine, and isopedine layers) and the plesiomorphic 'fish-like' sarcopterygian scale condition (i.e., rounded and/or rhombic cosmoid scales formed by two distinctive regions with a well developed basal isopedine layer) probably arose rapidly in tetrapods. This 'shift' in the squamation Bauplan, along with the appearance of digits, occurred during the Devonian and in an aquatic environment. These histological and morphological new features were maintained and almost unmodified during the terrestrialization and subsequent evolution of tetrapods during the Carboniferous. The retention of ossified dermal scales in early tetrapods attests that these Devonian forms had a benthic, strictly aquatic lifestyle and surely limited walking abilities.

Finally, the study of histological structures and detailed observations on scale morphology in sarcopterygians might furnish useful characters that would not only help elucidating the still debated phylogenetic interrelationships of tetrapodomorph fishes, but also shed more light on our understanding of the physiology and lifestyle of early tetrapods.

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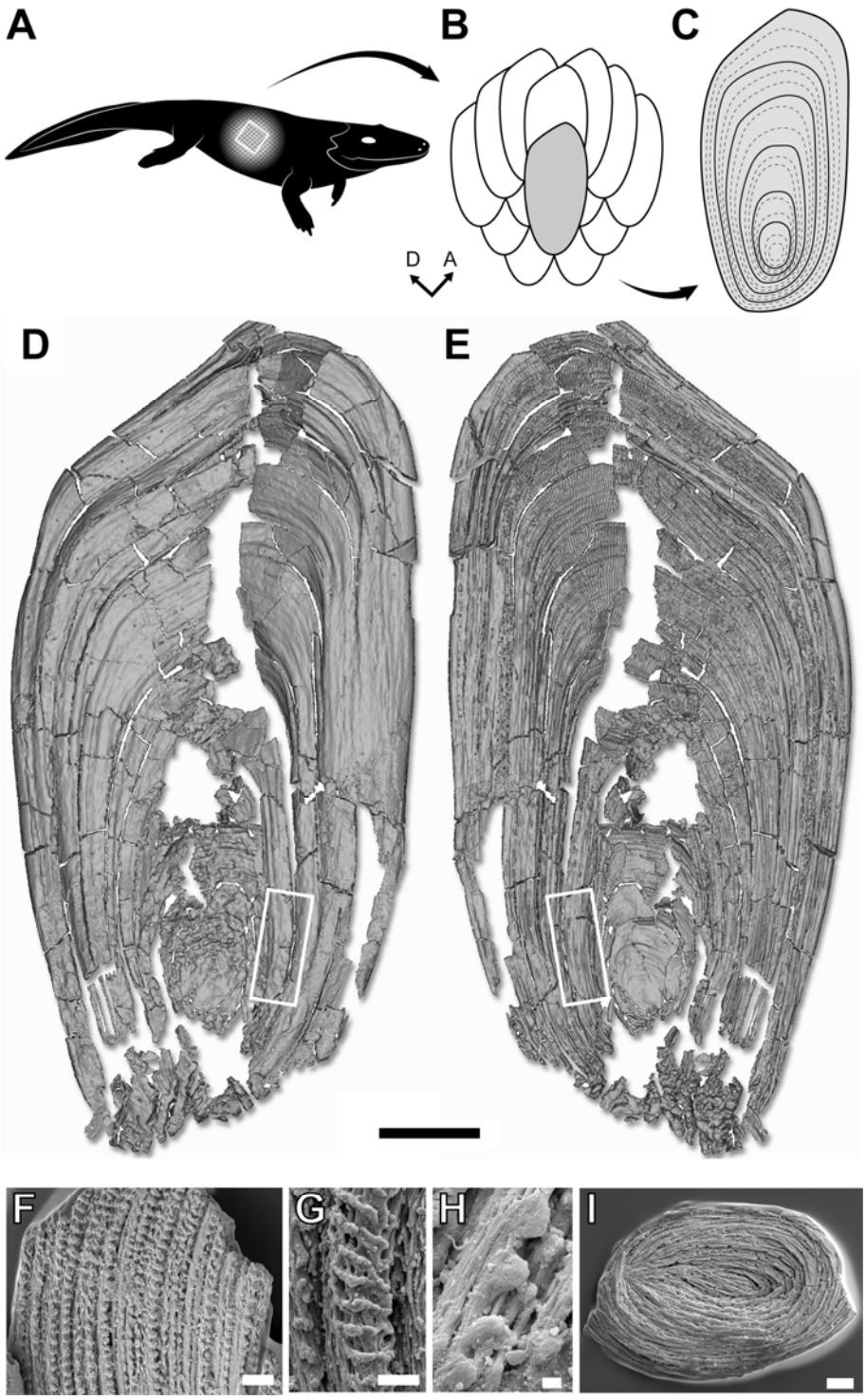
**FIGURE CAPTIONS**

**Figure 1**



The dermal scales of *Tulerpeton curtum*. Lebedev, 1984. **A**. Body outline of *Tulerpeton* with the relative position of the studied scales (right flank scales), **B**. overlapping pattern of the flanks scales, **C.** Schematical outline drawing of an isolated scale illustrating the arrangements of LACs (B,C redrawn and modified after Lebedev and Coates, 1995 according to the shape of the new modelled scale). **D,E.** Three-dimensional reconstruction of an ovoid scale of *Tulerpeton curtum* Lebedev, 1984 (PIN 2921/3238). **D**. External surface, **E.** Internal surface. Scale bar, 1 mm for D,E. **F-I.** SEM pictures of the scales of *Tulerpeton curtum* Lebedev, 1984 illustrating the ornamented internal surface. I. Rounded scale located in the limbs, in internal view. Scale bar, 100 μm (F,I), 50 μm (G), 10 μm (H).

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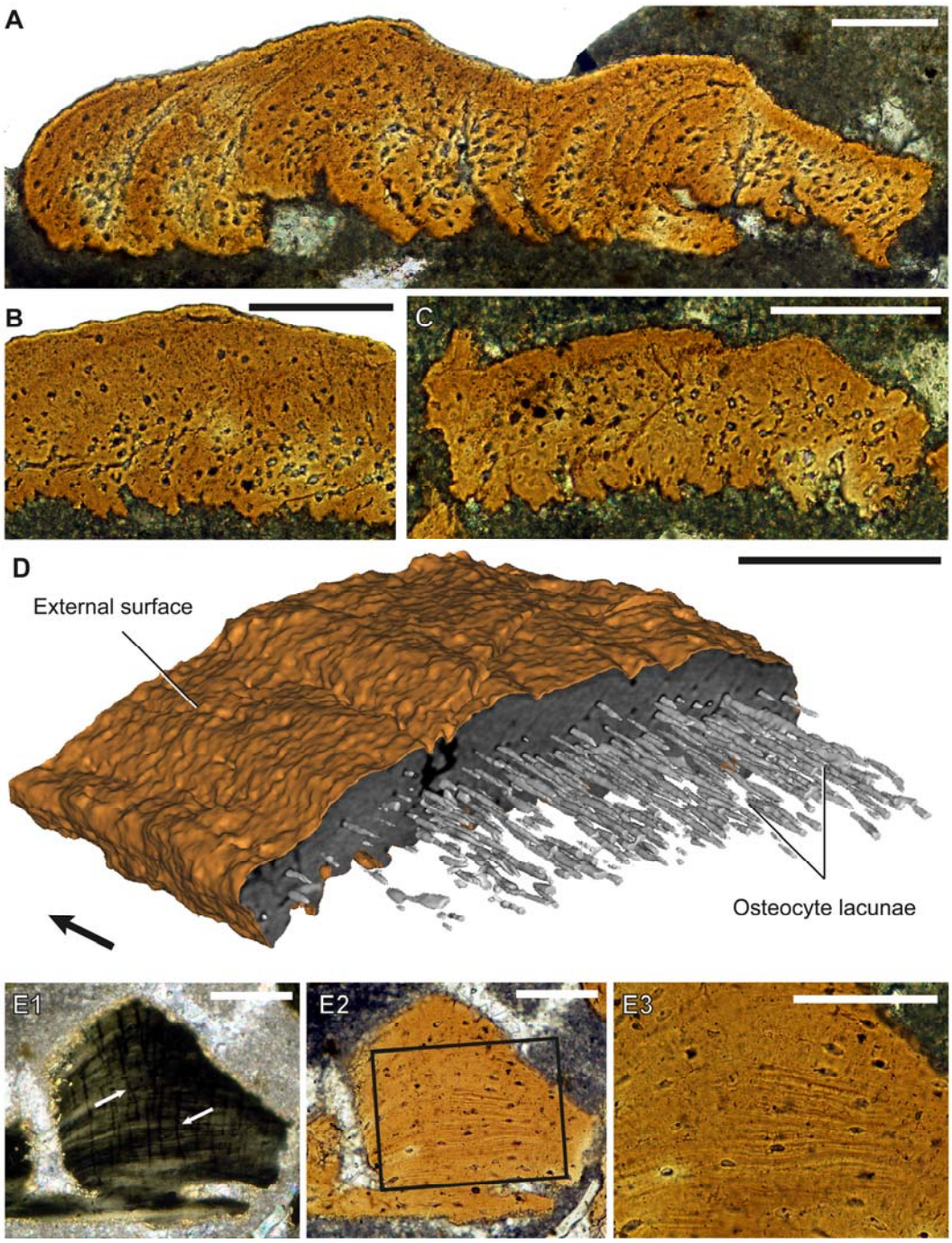
**Figure 2**



**A-C.** Insets of histological ground sections of the scales of *Tulerpeton curtum* Lebedev, 1984 (PIN 2921/3238) (see Supp. Figure 2). Note in **A** the growth 'waves' in the left lateral margin of the scale portion (A) and in the densely concentrated osteocytes in the internal (visceral) side of the scales **(**A, B, and C**)**. **D.** Combination of synchrotron microtomographic and histological data on an inset from the *Tulerpeton curtum* Lebedev, 1984 (PIN 2921/3238) modelled scale in Fig. 1 illustrating the density and arrangement of the osteocyte lacunae in the bone. Arrow points the main growth axis of the scale (antero-posterior). **E.** Insets of histological ground sections of the scales. **E1** illustrates the presence of Sharpey's fibers, pointed by arrows. **E3** corresponds to a magnified inset of **E2** showing the parallel fibres of the cellular bone. Scale bar, 100 μm. Scale bar, 100 μm.

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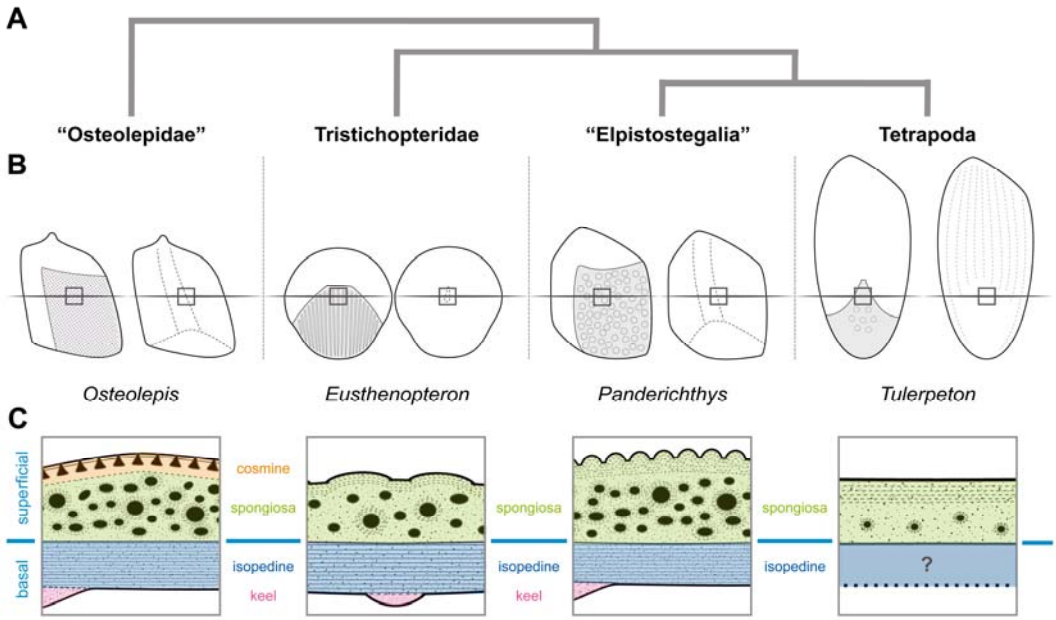
**SUPPLEMENTARY INFORMATION**

## Supplementary Figure 1




Schematic representation of the external morphology and histological structure of the scales in tetrapodomorph sarcopterygians. **A.** Currently accepted tetrapodomorph interrelationships (rhizodontids are considered the sister group of the depicted tetrapodomorphs but they are not represented here due to the lack of histological studies on their scales) (phylogenetic hypothesis after e.g., Cloutier and Ahlberg, 1996; Daeschler et al., 2006). **B.** External outline of the external (left) and internal (right) surfaces of the most representative tetrapodomorph scales for which histological cross sections have been performed. Note the presence in the exposed external surface (shaded in grey) of cosmine pores in *Osteolepis*, bony longitudinal ridges in *Eusthenopteron*, and bony tubercles in *Panderichthys*, and possibly in *Tulerpeton*. Lines represent cross section planes and squares are detailed as insets below. Scales not to scale but aligned to the same cross section plane. **C.** Schematic microstructural arrangement

of the different histological layers of the formerly presented scales separated into a superficial and a basal portion (*Osteolepis* after Gross, 1956 and new observations, *Eusthenopteron* after Zylberberg et al., 2010, *Panderichthys* after Witzmann, 2011; *Tulerpeton* after this study). Scale profiles and histological insets not to scale. Cosmine stands for the association of enamel and dentine pervaded by a pore-canal system; spongiosa stands for the vascular middle layer formed of pseudo-lamellar bone, typical of the sarcopterygian scale (note however that vascularisation can be more or less developed in different taxa, and that in the scales without cosmine, e.g., tristichopterids, "elpistostegalians" and tetrapods, the upper part of the spongiosa is more dense and less vascularized that in the core of the scale); isopedine stands for the basal layer of lamellar bone (mineralized or not) formed by a plywood-like arrangement of the collagen plies (note that in the scales of *Tulerpeton* and younger fossil tetrapods, the isopedine is not preserved due either to a complete loss of this layer or to a non mineralized isopedine not preserved in fossil specimens and hence it is marked here by a '?'); the keel stands for the basal most bony layer, formed of woven-fibered bone, that constitutes the articular ridge in rhombic scales of osteichthyans or the drop-shaped boss in the rounded scales of rhizodontids and tristichopterids.

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**VIDEOS**

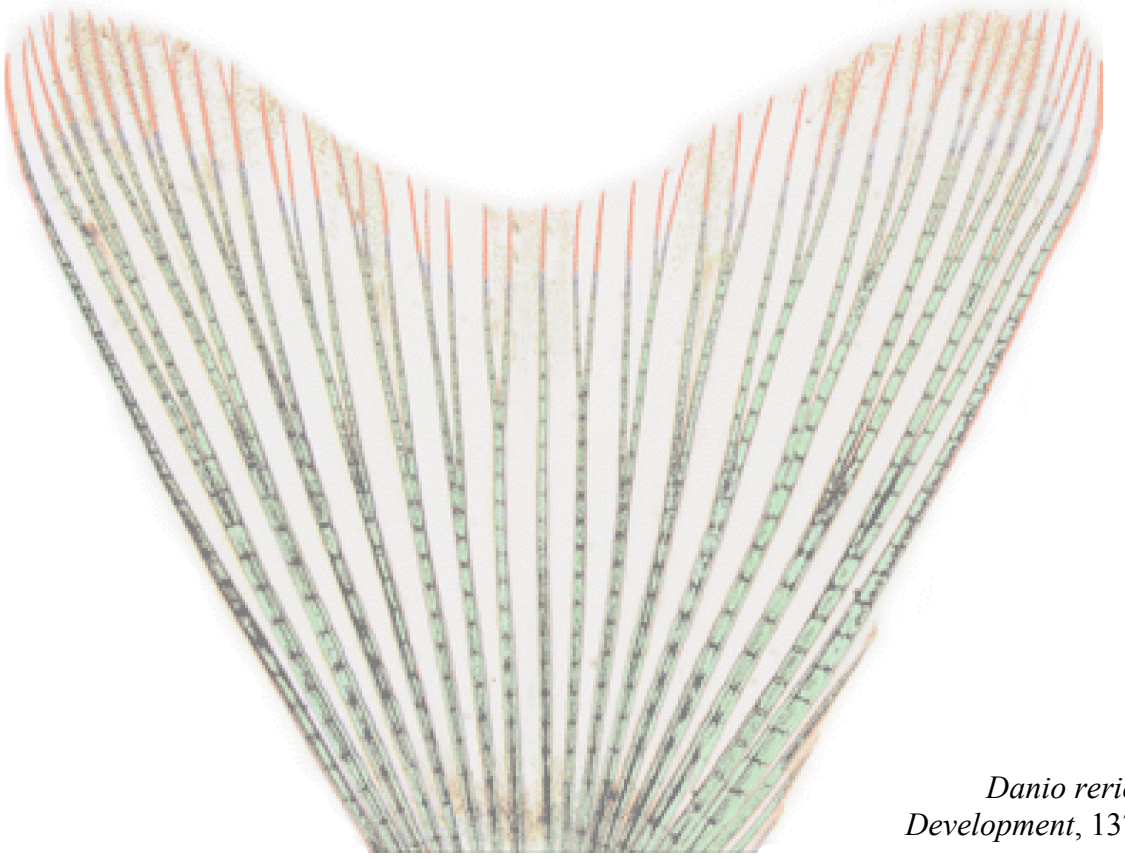
**Video 1**

360º view of the *Tulerpeton curtum* modelled scale.

**Video 2**

360º view of the scale inset from the *Tulerpeton curtum* modelled scale, illustrating the presence and arrangement of the osteocytes lacunae in the bone (seen be transparency).

# RESULTS
# –
# The Fin Rays



*Danio rerio*
*Development*, 137

## I. GENERAL INTRODUCTION

> *Almost every available character has been made use of in turn by systematists in the endeavour to classify the larger groups; and of these characters it is obvious that those which are based on structures capable of being fossilised must be the most useful. No parts of a fish are, as a rule, better preserved than the dermal skeleton. Yet, although Agassiz long ago classified fish into large divisions according to the structure of the scales, modern systematists are inclined to attach so little importance to the exo-skeleton that I venture to think they have somewhat neglected the dermal fin-rays.*
>
> GOODRICH, 1904

As for the scales, seen in the previous chapter, GOODRICH (1904) also attached a great deal of importance to the dermal fin rays, which he considered to be a valuable and most informative structure of vertebrate's anatomy. GOODRICH was among the first to realize than "crossopterygians" (i.e., fossil sarcopterygians) showed an important morphological diversity in fin and fin ray shape when compared to actinopterygians. However, this statement had only a minor influence in the development of the study of the sarcopterygian dermal skeleton throughout the twentieth century. Indeed, many anatomists considered the osseous fin rays (lepidotrichia) to show a rather stable and almost unchanged pattern in all osteichthyans. Nevertheless, there are some striking differences in arrangement, number, and structure of the lepidotrichia in diverse groups of bony fishes that deserve to be described and interpreted in the light of new paleontological and genetic discoveries. Moreover, the establishment of the zebrafish as a model organism in the study of vertebrate development now offers the opportunity to experiment with the fin rays. This may lead to a better understanding of their formation, morphology, and functional and ecological implications in the evolution of osteichthyans.

This chapter comprises a long review article on the diversity of dermal fin rays in osteichthyans (Paper IV). Special importance will be given to new developmental genetic hypotheses of fin ray patterning and formation. The establishment of fin rays as developmental and evolutionary modules in osteichthyans could shed more light on the transition from fins to limbs in Devonian tetrapods.

**IV** **Mondéjar-Fernández, J.**, Marí-Beffa, M., Arratia, G., Clément, G. & Janvier, P. Diversity of dermal fin rays in Osteichthyes, evolutionary developmental evidence, and the 'fish-tetrapod transition'. Manuscript.

The Paper IV is currently in progress. I have written the majority of the herein presented version of the article, including the introduction, nomenclature, sarcopterygian and discussion parts. I also produced all the figures (except fig. 5, in which the drawing was provided by Manuel MARÍ-BEFFA) and shared the interpretation and discussion of results. I am still waiting for the contribution of the other co-authors to perform the process of homogenisation of the writing

## DIVERSITY OF DERMAL FIN RAYS IN OSTEICHTHYES, EVOLUTIONARY DEVELOPMENTAL EVIDENCE, AND THE 'FISH-TETRAPOD TRANSITION'

As previously described, the dermal fin rays in osteichthyans are of two types: fibrous fin rays (the actinotrichia) and osseous fin rays (the lepidotrichia). The actinotrichia precede the lepidotrichia and their presence of the former in the early stages of fin development is necessary for the formation of the latter. This condition has been well known for several decades (e.g., GÉRAUDIE & LANDIS, 1982; DURÁN *et al.*, 2011) but very few works have dealt with the description of the adult morphological and structural diversity of the bony fin rays, and even fewer works considered their evolutionary importance and implications in osteichthyans. The recent progress and application of conclusions from developmental genetics to the understanding of paleontological and evolutionary issues offers a new opportunity to study the fin rays under a much larger frame.

One of the principal starting points for every study on evo-devo is the recognition of morphologies that could be informative on the developmental processes underlying the formation of the studied structure (in our case, the fin/limb development). The now well-documented fossil record of Devonian sarcopterygians broadens the range of fin morphologies already known in osteichthyans. Although most of the former studies and reviews including both paleontological and developmental evidences have considered the fin endoskeleton (CLACK, 2009a; SHUBIN *et al.*, 2009), the focus on the fin ray diversity was somewhat attenuated and cited merely as a consequence of endoskeletal expansion in the fins of tetrapodomorphs.

When I first began to consider how to develop an evo-devo focus research on fin rays, I realized that I would need an anatomical and evolutionary reference framework before starting any experiment on fin ray development. Upon this phylogenetic and developmental framework, I could apply any treatment and explain the expected results. Along with my supervisor Manuel MARÍ-BEFFA, we decided to focus on the writing of a complete review on fin and fin ray morphologies in osteichthyans. By integrating the large diversity of shapes and structures of the fin rays, especially of fossil sarcopterygian taxa, we would more deeply comprehend the process of fin and fin ray formation and identify the 'spots of variability' responsible for the morphological diversity seen in the fossil record. I naturally focused on sarcopterygians and I personally took the initiative to contact the world-renowned specialist on actinopterygians Gloria ARRATIA to include her among the co-authors to write the part on fossil actinopterygians.

The main aim of this article was to review all kinds of fibrous and osseous fin rays in osteichthyans and to use these evidences to propose a new reference framework. This framework would hopefully drive future research in developmental biology of fin formation. Once finished, I could resume my experimental work on zebrafish and apply our observations of fossil diversity to new laboratory studies focusing in key molecules. After perturbing these molecules, the morphological consequences could parallel the divergent morphologies seen in the fossil record. This new work would have been included in a second paper on fin rays under a pure evo-devo methodology. Eventually and unfortunately, the process of revision was longer and more complicated than I expected. My will to finish this review before digging completely into the new the evo-devo paper somehow delayed its writing and the exploitation of experimental results that were already acquired at the Málaga University.

The manuscript version of the review paper herein presented is thus unfinished. The current contribution of each co-author is given in brackets, next to the title of the respective parts. The final version of the article will logically need considerable shortening and homogenisation of the writing style, as well as addition of new figures and parts in the discussion including the data on fin ray patterns of actinopterygians. Preliminary figures are included in the Figure Captions section at the end; the numbering is provisional.

Most of the descriptive sections on sarcopterygians (generalities, phylogenetic positions and fin patterns) have already been presented in the introduction and I warn the reader on the occurrence of certain repetitions. Nevertheless, the parts concerning fin ray arrangement and structure for every sarcopterygian group are original and constitute the core of each description.

# Paper IV

**Diversity of dermal fin rays in Osteichthyes, evolutionary developmental evidence, and the 'fish-tetrapod transition'**

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Manuscript in preparation with co-authors

Considering submission to: *Zoological Journal of the Linnean Society*

*Journal of Morphology*

*Journal of Anatomy*

**ABSTRACT** (Jorge MONDÉJAR-FERNÁNDEZ)

The dermal fin rays of the Osteichthyes (bony fishes) play a major morphofunctional role in aquatic locomotion. However, knowledge on the morphological, structural, and developmental diversity of fin rays is incomplete in both groups of bony fishes, the actinopterygians (ray-finned fishes) and the sarcopterygians (lobe-finned fishes).
The different types of fin rays of fishes (dermotrichia) comprise osseous rays (lepidotrichia) and non-mineralized collagenous rays (actinotrichia and ceratotrichia). Osteichthyans possess actinotrichia and lepidotrichia. The actinotrichia form the larval fin fold and are later replaced by the lepidotrichia as the main dermal fin rays in adult fins.

Sarcopterygians show a greater diversity of form, structure and arrangement of the osseous lepidotrichia than the actinopterygians. This diversity comprises segmented and distally bifurcated lepidotrichia (the common osteicthyan condition), long unsegmented lepidotrichia (in rhizodontids and Devonian tetrapods) and modified, partially mineralized lepidotrichia (the so-called camptotrichia of dipnoans). Morphological diversity among sarcopterygians can be explained by subtle changes affecting the three developmental axes of fin and fin ray formation (proximo-distal, antero-posterior, and contralateral). These changes concern in particular the establishment of the segmentation and bifurcations patterns of the rays, their position in the fins, and the relationship between radial bones and lepidotrichia.

In this review, the nomenclature used to define the main morphotypes fin rays in vertebrates will be presented in order to describe in detail the diversity of rays in osteicthyans. A survey of the morphology and development of these rays would allow us to propose an evolutionary and developmental model relative to the morphological diversification of the lepidotrichia. Eventually, this model would be to the question of the enigmatic maintenance and loss of fin rays in early tetrapods.

## INTRODUCTION (Jorge MONDÉJAR-FERNÁNDEZ)

The vertebrate skeleton is divided in two distinct systems with different developmental and phylogenetic origins: the endoskeleton and the dermoskeleton (Patterson 1977). The dermal skeleton was the first to appear in a mineralized form in vertebrates (Janvier, 1996) and is primitively the most extensively developed in 'agnathans' (with the exception of lampreys and hagfishes) and early gnathostomes (Donoghue, 2002; Donoghue & Sansom 2002).

The dermoskeleton is formed by two main components: a dental (odontogenic) unit composed of dentine, bone of attachment and enamel (or enameloid in some taxa), and osseous (osteogenic) unit comprising an underlying layer of dermal bone that can be differentiated into spongy or cancellar bone overlying a basal lamellar bone layer. It can be noted that the dermal skeleton does not exhibit great variability in its composition; however the structural arrangement and distribution of the different tissues can be quite variable (Donoghue & Samson, 2002). The dermal skeleton comprises the scales distributed along the body, several dermal bones of the skull (dermocranium), the teeth and denticles located in the mouth cavity, and the fin rays.

The dermal fin skeleton is one of the key structures related to the success and diversification of bony fishes (Osteichthyes) enabling diverse morphofunctional adaptations to different habitats and ways of life. Indeed, the dermal fin rays are one of the most important functional elements related to aquatic locomotion (Webb, 1984, 1988). In fishes, fin rays of both paired and median fins are arranged into a fins webs that are the largest flexible and mobile surfaces of the body. These fin webs are hydrodynamic control surfaces, enhancing trust production and generating off-axis forces during swimming, enabling the fish to develop high manoeuvrability and triggering propulsion (Lauder & Drucker, 2004).

A fin can be described as a membranous lateral outgrowth of the body walls reinforced internally by elongated elements. These internal reinforcements can be of endoskeletal (e.g., radial bones) or dermoskeletal (dermal fin rays) nature. In vertebrates, fins may exclusively show dermoskeletal elements (i.e., dermal fin rays as in the earliest vertebrates; Shu et al., 1999, or in the early development of extant gnathostomes; Kimmel et al., 1995). Fins may also exclusively present endosqueletal elements (e.g., the tails of cetaceans), or both endoskeletal and dermoskeletal (e.g. the fins of the extant actinopterygian fishes). When endosqueletal and exosqueletal structures are present together the fin rays of all paired and unpaired fins cover the most distal part of the endoskeletal elements.

The fin pattern of early aquatic vertebrates is rather constant; the fins can be divided in two different fin sets: paired fins (pectoral and pelvic fins) and unpaired fins (dorsal(s), anal, and caudal). The paired fins are further classified into pectoral and pelvic fins located lateroventrally on each side of the body. The unpaired or median fins are positioned along the dorsal [dorsal fin(s)] and ventral (anal fin) midline of the body. Although this fin pattern is very common, the number of fins can be variable. This may specially be observed in the multiple dorsal and ventral finlets located in front of the caudal fin of certain actinopterygians (e.g., *Polypterus*). The caudal (or tail) fin is contralaterally flattened in the posterior end of the body and constitutes the main source of propulsion forces for swimming.

The different types of fin rays of fishes are gathered under the name dermotrichia (Goodrich, 1904) in connection to their origin and ossification. Among dermotrichia, there are osseous rays, like lepidotrichia and camptotrichia (the latter, only present in lungfishes), and non-mineralized collagenous rays, such as actinotrichia (in Osteichthyes) and ceratotrichia (in Chondrichthyes) (see Nomenclature for further details).

The Osteichthyes (bony fishes) comprise two major groups, the Actinopterygii (ray-finned fishes) and the Sarcopterygii (lobe-finned fishes, including the Tetrapoda). In

chondrichthyans (i.e., sharks and skates) and other early gnathostomes (e.g., placoderms) the fin rays are mainly fibrous (non mineralized) in all ontogenetic stages. In osteichthyan larvae, the fins are supported by fibrous, horny rays (the so-called actinotrichia), whereas in adult fins the fibrous rays are replaced by osseous rays primarily composed of a combination of osteogenic and odontogenic cell products, i.e., bone covered with dentine and enamel respectively (the so-called lepidotrichia). These two outer layers of dentine and enamel tend to disappear during the evolutionary history of osteichthyans, but are still present in stem actinopterygians ("paleonisciforms") and Devonian sarcopterygians (e.g., porolepiforms and "osteolepidids"). In sarcopterygians, enamel and dentine layers are no longer present in the dermoskeleton of holoptychiids, rhizodontids, derived "osteolepiforms", and post Devonian lungfishes (Jarvik, 1959). Osseous fin ray-like scales arranged into parallel oblique rows are present in some jawless vertebrates (osteostracans and anaspids) (Janvier, 1996; Coates, 2003; Janvier et al., 2004). These scales have been formerly proposed to be the precursors of the osseous fin rays of osteichthyans (Jarvik, 1959), but they are currently interpreted as a convergent structures (Friedman & Brazeau, 2010).

Despite a long history of research in fossil osteichthyans (e.g., Agassiz, 1833-44; Williamson, 1849; Schaeffer, 1968), fins and fin rays have received little attention. This was mainly due to the delicate nature of fin rays and its subsequent poor preservation in the fossil record. Moreover, the description of "general" features of the fin rays in osteichthyans (see below) have been taken for granted in most descriptions and resulted in a neglected detailed illustration of the structural diversity of the fin rays in many taxa. Accordingly, it is sometimes difficult to understand the choices made by several authors in schematic representations or restorations of the fins and fin rays of fossil specimens. Students and readers interested in osteichthyan fishes (fossil or extant) are thus in need of a thorough revision of the structure, morphological diversity, and evolution of the dermal fin rays.

The aim of our study is to provide a revised interpretation of key fossil specimens by a profound revision of the literature concerning fins and fin rays in vertebrates. In this review we will first introduce the main nomenclature used to define the different fin ray structures in fishes in order to describe more accurately the diversity of the bony fin rays in osteichthyans. A throughout revision of the morphology and development of these rays will allow us to propose a developmental and evolutionary pattern of formation and morphological diversification of the fin rays in the bony fishes. This could eventually shed light on the puzzling question of the origin, maintenance and even loss of the fin web in fishes and early tetrapods.

## NOMENCLATURE (Jorge MONDÉJAR-FERNÁNDEZ)

### Lepidotrichia

The term lepidotrichia (from the Greek “lepis”=scale and “trichium”=thread) was first coined by Goodrich (1904) to name the bony fin rays of Teleostomii [Crossopterygii and Actinopterygii *sensu* Goodrich (1904)]. Later, lepidotrichia were considered to constitute a synapomorphy of crown osteichthyans (Schaeffer, 1968; Rosen et al., 1981; Lauder & Liem, 1983; Gardiner, 1984; Maisey, 1986; Friedman & Brazeau, 2010). Lepidotrichia were thus likely to be present in the paired and median fins of all Paleozoic bony fishes (Janvier, 1996), ranging from actinistians, fossil Devonian lungfishes, and other sarcopterygians, to fossil and extant actinopterygians.

The lepidotrichia are osseous dermal fin rays. Each lepidotrichium is composed of two parallel and symmetrical bony elements in the shape of a parenthesis. In a lepidotrichium, these bony elements have been called demirays (Kemp & Park, 1970), hemisegments (Lanzing, 1976), hemilepidotrichia (Géraudie & Landis, 1982), or hemirays (Murciano et al.,

2007). From this point on, we will use the term hemilepidotrichia to avoid confusion between hemisegments and lepidotrichial segments (see below) and support Goodrich's original term. The two rows of symmetrically arranged hemilepidotrichia become concave towards the distal portion of the ray (e.g., in the caudal fin of the actinopterygian *Xiphophorus*, and in the paired fins of the sarcopterygian *Eusthenopteron*) (Goodrich, 1901, 1906; Becerra et al., 1983). Both hemilepidotrichia delimit an inner tissue that house blood vessels and nerve fibres, plus connective tissue cells (Géraudie & Landis, 1982; Becerra et al., 1983; Durán et al., 2011). At the distal tip of the lepidotrichia, collagenous fin rays (actinotrichia, see below) are organized in two bundles between both hemilepidotrichia resembling a bilaminar painter's brush (Becerra et al., 1983).

The bone forming the lepidotrichia can be acellular (without enclosed osteocytes) or cellular (with osteocytes enclosed in the matrix). In the sarcopterygian *Eusthenopteron* the proximal region of the lepidotrichia is formed by cellular bone whereas the distal one is formed by acellular bone (Zylberberg et al., 2010). The actinopterygian *Polypterus* presents only cellular bone (Géraudie, 1988), whereas in other actinopterygians, cellular bone can be deposited by apposition surrounding the initial acellular matrix during growth (Lanzing, 1976; Géraudie & Landis, 1982). It has been proposed that the term lepidotrichium stands for the characteristic dermal bone forming the fin rays, and not the ray *per se* (Marí-Beffa & Murciano, 2010). As originally proposed by Goodrich (1904), here we will restrict the term lepidotrichia and lepidotrichium to describe the dermal fin rays as a complex and regionalized morphological structure.

Normally, lepidotrichia are segmented (i.e., "jointed" lepidotrichia), forming a series of repetitive elements that are connected together by fibrous collagenous ligaments called Sharpey's fibers (e.g., in the actinopterygians *Tilapia, Carassius, Thunnus, Serrasalmus*, and *Cyprinus*, among others, and in the sarcopterygians *Latimeria* and *Eusthenopteron*) (Castanet

et al., 1975, Becerra et al., 1983; Zylberberg et al., 2010). The "joints" correspond to very narrow, non-mineralized spaces occurring between adjacent segments (Géraudie & Meunier, 1984; Zylberberg et al., 2010). The most proximal segment articulates with the endoskeletal elements of the fin and is always longer than the others from the very first stages of development. According to the revised literature, this is observed in all known osteichthyans where the fins have been studied (e.g., the actinopterygians *Gobius*, *Pygosleus, Cottus,* and *Blennius,* among others, and the sarcopterygians *Miguashaia* and *Eusthenopteron*; François & Blanc, 1956; Cloutier, 1996a; Cote et al., 2002). In some instances, this proximal segment then grows by fusion with the distally neighbouring segments enlarging its lenght (François & Blanc, 1956, but see Haas, 1962 for another interpretation in the actinopterygian *Trichogaster*). This may occur by an erasing deposition of new lepidotrichial matrix over the joints (see Murciano et al., 2007). Adjoining segments are sequentially added distally during appositional growth of the lepidotrichium (Prenant, 1936) whereas ossification of the rays begins proximally. In any case, segmentation of the lepidotrichia occurs prior to their ossification in species showing proximally segmented rays in their fins (e.g., in the actinopterygian *Oncorhynchus*; Charest & Cloutier, 2009). The occurrence and pattern of segmentation of the lepidotrichia are considered ontogenetic characters useful to determine growth series, especially in fossil taxa (e.g., in the sarcopterygians *Miguashaia* and *Eusthenopteron*; Cloutier, 2010). Segmented lepidotrichia are the rule rather than the exception, and represent the plesiomorphic state among osteichthyans (Schaeffer, 1968).

In their most distal portion, the lepidotrichia usually bifurcate (i.e., branched lepidotrichia) as if the ray was split in two. The branching of the lepidotrichia is due to the repeated subdivision of the distal portion of the ray during its growth (Goodrich, 1904). Each lepidotrichium can show up to three or four orders of distal bifurcations (e.g., in the sarcopterygians *Holoptychius* and *Eusthenopteron*, and in the actinopterygian *Danio*) (Jarvik,

1980; Grandel and Schulte-Meker, 1998). Bifurcation of the lepidotrichia constitutes the last stage in fin ray development (Laforest et al., 1998) and can also be considered as an ontogenetic character. Also, within one species, branched and unbranched lepidotrichia can coexist within one fin (e.g., the first and the last of the principal rays and the procurrent rays in the caudal fin in teleost never branch; Arratia, 2008). Following experimental analysis during fin development and regeneration, ray branching has been proposed to depend on distal interactions with neighbouring interray tissues (Murciano et al., 2002; Murciano et al., in preparation). This has led Marí-Beffa and Murciano (2010) to suggest a new anatomical concept, the *pinnamere*, (form the Latin "pinna"=fin; "mere"=unit) to define the ensemble of a ray and both neighbouring half interrays.

Bifurcation of the lepidotrichia is the last ontogenetic feature visible during fin development in osteicthyans (Charest & Cloutier, 2009), and therefore epigenetic of positional phenomenons are more susceptible of suppressing the bifurcation (see discussion). The absence of bifurcation is a convergent character among osteicthyans. The occurrence or absence of bifurcation is dependent on the position of the lepidotrichia in the fin (e.g., the anterior most lepidotrichia of the dorsal, anal and caudal fins in actinopterygians are usually unbranched) (Arratia, 2008).

Certain lepidotrichia can lack either segmentations or bifurcations, or both (i.e. unsegmented and unbranched lepidotrichia). Unsegmented lepidotrichia show a large range of morphologies in osteichthyans, especially in actinopterygians where they can form spines or spiny rays in the anterior most ray(s) of the pectoral, dorsal and anal fins. These characters are apomorphies of a variety of actinopterygian families belonging to Perciformes, Siluriformes, or Acanthopterygii clades (Francillon-Vieillot et al., 1990; Arratia, 2008). In these fishes, the spine is considered either as an ontogenetic fusion between the two hemilepidotrichia of a lepidotrichium (e.g., actinistians), a fusion of several lepidotrichia (e.g.

sturgeons), or a modified lepidotrichium (e.g., cyprinids and silurids; Arratia, 2008). Usually, there is no actinotrichia in the distal end of the spine in adult specimens. In small ones, actinotrichia are still present (Arratia, 2008). Among sarcopterygians, the lepidotrichia of some Devonian actinistians and early tetrapods are neither segmented nor bifurcated (see below). It has been proposed that bifurcation of the lepidotrichia only happens in already segmented rays (Cloutier, 1996a). Bifurcation alone seems to be an impossible morphological condition in sarcopterygians.

The lepidotrichia articulate with the most distal endoskeletal elements (radials or pterygiophores) in the paired and median fins. The hemilepidotrichia are contralaterally arranged in both sides of the endoskeleton elements (left and right for the median fins, dorsal and ventral for the paired fins), with their proximal tips embracing the distal end of the radials. Usually, each radial carries more than one lepidotrichium, however certain derived groups (e.g., teleosts and actinistians) show a 1:1 ratio between the radials and the fin rays (see below). When present in osteichthyans, the lepidotrichia are able to regenerate after injury or ablation (Broussonet, 1786; Francillon-Vieillot et al., 1990).

Lepidotrichia are composed of mineralized, parallel-fibered bone, and the matrix probably contains collagen type I (Géraudie and Landis 1982). Besides, type II, type X and type XI (Padhi et al., 2004) and fish-specific collagens (Durán et al., 2011) have been shown to occur in the fins of the zebrafish. This combination has led Marí-Beffa et al., (2007) to suggest a particular skeletal nature to the lepidotrichia different to cartilage, bone, enamel or dentine. Moreover, the orientation of the collagen fibrils enables to indentify different layers. Becerra et al. (1983) identified three zones in the teleost *Tilapia*: an outer zone with parallel running fibers, a transition zone, and an older inner woven-fibered zone. In polypterid actinopterygians only two zones are known: an outer zone made of woven bone, and an inner one made up of lamellar bone (Géraudie, 1988). In sarcopterygians, such as *Eusthenopteron*,

concentric layers of lamellar bone are distributed homogenously along each lepidtrochium (Zylberberg et al., 2010).

The lepidotrichia form in the basement membrane that separates the epidermis from the underlying mesenchyme. They differentiate within the extracellular collagenous basal lamella of the epidermal-dermal interface and subsequently become progressively separated from the epidermis by the invasion of mesenchymal cells. Following this invasion, the lepidotrichia detach completely from the basement membrane and penetrate into the mesenchyme of the dermis where they are surrounded by mesoblastic tissue (François, 1958; Géraudie & Landis 1982; Sire & Huysseune, 2003). These outer invading cells may synthetize the outter zone (Becerra et al., 1983) generating a symmetrical structure. According to Géraudie and Landis (1982), both epidermal and mesenchymal cells are involved in the process of lepidotrichial differentiation. During the first stages of formation, lepidotrichia are composed of acellular bone. Later, osteoblasts can become incorporated to form cellular bone around the initial acellular matrix (Meunier, 1987). Becerra et al. (1983) suggest that the cellularity (the amount of enclosed osteocytes) of the bone depends on the thickness of the hemilepidotrichium. Once it is formed, distal elongation of the lepidotrichium is accomplished by terminal growth and ossification.

Lepidotrichia and scales of primitive actinopterygians and sarcopterygians are often structurally similar and can be covered on their external surface with an enamel (or enameloid) and dentine layer. The lepidotrichia can thus show a histological structure similar to that of the scales, hence their name. For example, the outer surface of the fin rays of the basal extant actinopterygians (*Lepisosteus, Polypterus,* and *Calamoichthys*) and) are covered with a ganoin layer and denticles (Géraudie & Landis 1982; Géraudie, 1988). Moreover, extant actinistians (*Latimeria*) retain a series of dentine denticles in the scales in lepidotrichia (see below). In Paleozoic sarcopterygians, the lepidotrichia of cosmine-bearing

porolepiforms, dipnoans and “osteolepiforms”, are covered with enamel and dentine showing the same histological structure as the cosmine of their scales (Thomson, 1975; Meinke, 1984). In more derived actinopterygians (Amiiformes and Teleostei) and sarcopterygians (by convergence in almost all groups), the lepidotrichia loose the dentine and enamel covering and retain solely the inner region of the ray formed by true bone (Goodrich, 1904).

Early studies on fin ray development (e.g., Baudelot, 1983; Goodrich, 1904 and references therein) put forward the homology between lepidotrichia and scales, since they were considered to share the same structure, the same type of development and, therefore, the same ontogenetic origin. Goodrich (1904) and Jarvik (1959) supported this hypothesis on the basis of the histological similarities and morphological transformation between scales and fin rays, highlighted by the condition seen in sarcopterygian “osteolepidids” like *Gyroptychius*. However, this condition does not necessarily imply that the lepidotrichia are modified scales, or that lepidotrichia evolved *directly* from scales. To Schaeffer (1977: 44) it is perhaps more meaningful to consider that “scales and lepidotrichia composed of enamel, dentine and bone are somewhat different morphological manifestations of the same morphogenetic system”. It is thus possible that the classical scenario of a mere transformation of scales into lepidotrichia could be more complex than it is currently depicted.

**Camptotrichia**

The term camptotrichia (from the Greek “campto”=curved or flexible and “trichium”=thread) was proposed by Goodrich (1904) to describe the peculiar dermal fin rays of dipnoans, which show a different structure from that of the lepidotrichia. Camptotrichia derive from lepidotrichia and are a synapomorphy of the Dipnoi. They are present in the extant lungfishes *Neoceratodus, Protopterus* and *Lepidosiren* where they display the same function as the lepidotrichia of other osteichthyans (Géraudie & Meunier, 1982).

Camptotrichia outnumber the endoskeletal fin elements; in the same way as the lepidotrichia do in certain osteichthyan groups (see above).

The camptotrichia are flexible dermal fin rays usually segmented and distally branched (except in the extant *Lepidosiren*; Arratia et al., 2001). They lie within the fin web, closely arranged in parallel, and they are separated by mesenchymal cells permitting an exceptional degree of flexibility (Géraudie & Meunier 1982, 1984).

The camptotrichia are divided in two different parts: [1] a superficial (subepidermal in origin) osseous region formed by either acellular bone tissue (in *Protopterus*) or cellular bone tissue (in *Neoceratodus*), and [2] a deep underlying (dermal in origin) fibrous region, continuous with the previous one, formed by a collagen-rich tissue. This deep region shows no calcification and is considered as a bone derivative that has lost the ability to mineralize and, accordingly, would remain in a "pre-bone", collagen-rich state (Géraudie & Meunier, 1984; Meunier, 1987). The only ossified region of the camptotrichia is the external one, corresponding to the outer portion of a hemilepidotrichia in other osteichthyans.

Goodrich (1904) and Jarvik (1959) proposed that camptotrichia evolved in lungfishes from completely ossified rays, similar to lepidotrichia. In this sense, it has been claimed that camptotrichia would merely be hemilepidotrichia that have lost their symmetry due to non ossification of their internal surface (Francillon-Vieillot et al., 1990). Géraudie and Meunier (1984) proposed that, unlike lepidotrichia, camptotrichia do not show "hemicamptotrichia" (i.e., demirays or hemirays; see above). Accordingly, a camptotrichium would be homologous to a hemilepotrichium. In our opinion, these considerations would lead to an unnecessary nomenclatural confusion between camptotrichia, hemilepidotrichia, lepidotrichia, etc. In this article, we will refer to the camptotrichia in the same way as to the lepidotrichia. A lepidotrichium is formed by two hemilepidotrichia in other osteichthyans, a camptotrichium stands for the couple formed by the two demirays in dipnoans.

**Actinotrichia**

The term actinotrichia (from the Greek “actino”=ray and “trichium”=thread) was first used by Ryder (1886) to describe the flexible fibrous elements located at the distal end of the lepidotrichia in actinopterygians. These rays are present in all extant actinopterygians, in the coelacanth *Latimeria* (Géraudie & Meunier, 1980), but absent in extant adult dipnoans (Goodrich, 1904; Géraudie & Meunier, 1982, 1984), although they are present in early stages of their ontogeny (Arratia et al., 2001).

The actinotrichia are short, thin tapered, fibrous rays that are not derived from bone (i.e., “horny” rays). They are usually unsegmented and undivided but they may however be segmented and branched at their distal end. They are formed by long fibres of collagen known as elastoidine (Durán et al., 2011) and they are considered homologous to the ceratotrichia of chondrichthyans (see below).

The actinotrichia form the main support of the osteichthyan fins in larval and juvenile stages of the ontogeny and are found in the most distal part of the adult fins arranged in contralateral palisades. In polypterid finlets, they can also be oriented perpendicularly to the long axis of the fin (Géraudie, 1988). Actinotrichia are present in most extant actinopterygians and sarcopterygians where they are replaced by the lepidotrichia as the main rays in the developing fin. Exceptions to this can be found in the adipose fins of some teleosts (e.g., Salmonidae, Siluriformes) where actinotrichia are retained in adult specimens (Goodrich, 1904; Brohl, 1909), or in polypterids where they have been reported in the joints between adjacent lepidotrichial rays (Géraudie, 1988). Actinotrichia formation is essential for the development of the lepidotrichia (Géraudie & Landis, 1982; Santamaría & Becerra, 1991; Durán et al., 2011) but do not give rise to the latter by coalescence or differential growth (Goodrich, 1904). Indeed, the collagenous actinotrichia would constitute directive precursors

of the development of the bony lepidotrichia despite their different origin and development (Géraudie & Landis, 1982 *contra* Goodrich, 1904).

The actinotrichia are smaller, more numerous than the bony rays, and are located in bundles at the distal tip of the fins. They are sandwiched by the hemilepidotrichia or overlapping them in adult specimens. During the formation of the lepidotrichia, actinotrichia are progressively resorbed, both within hemilepidotrichia and between lepidotrichia, leaving only a narrow distal fringe visible in all extant actinopterygians (except in polypterids, see above), and in the living coelacanth *Latimeria* (Géraudie & Meunier, 1980). Actinotrichia have not been observed within camptotrichia in adult stages of the development in extant dipnoans (Goodrich, 1909) implying that actinotrichia are completely resorbed during the formation of the camptotrichia (Géraudie & Meunier, 1984). Actinotrichia are also able to regenerate after ablation (Francillon-Vieillot et al. 1990).

Actinotrichia develop within the median and paired fin folds, first in the fin bud apex and later reaching the base of the fin fold (François, 1958; Géraudie 1977; Géraudie & Landis 1982; Durán et al., 2011). Actinotrichia are synthesized by both the epidermis and the mesenchyme, but they develop initially without the participation of mesenchymal cells and their collagen is exclusively secreted by epidermal cells (Géraudie, 1977, 1980, 1981; Durán et al., 2011). Mesenchymal cells nevertheless regulate the final growth in length and width of the actinotrichia (Géraudie 1977; Durán et al., 2011). The formation of actinotrichia is followed by the appearance and development of the cartilaginous endoskeletal elements (e.g., radials, neural spines, epurals, haemal spines, and hypurals), and the formation of the lepidotrichia (Géraudie and Landis 1982; Cubbage and Mabee 1996; Borday et al. 2001; Mabee et al. 2002). Mesenchymal cells (osteoblasts) may then use the actrinotrichia as a scaffold during the initial stages of formation of the lepidotrichia (Géraudie and Landis, 1982; Santamaría and Becerra, 1992; Durán et al., 2011).

Actinotrichia are also able to regenerate after ablation (Francillon-Vieillot et al., 1990). During fin regeneration, actinotrichia are synthetized and maintained in distal positions (Krukenberg, 1885; Durán et al., 2011). During distal maintenance, actinotrichia resorbtion has been experimentally proven by radioactive labelling of elastoidin (Marí-Beffa et al., 1989).

Actinotrichia were most likely to be present in basal sarcopterygians and very probably at the origin of osteichthyans (Patterson, 1977). Unfortunately, actinotrichia do not fossilize (or only exceltionally) due to their fibrous nature. Therefore, it is difficult to affirm that they were present in all groups of fossil sarcopterygians. Nonetheless, since extant actinopterygians and actinistians (*Latimeria*) maintained them until recent times, it is highly improbable that certain basal sarcopterygians would not have done differently (see below).

**Ceratotrichia**

The ceratotrichia (from the Greek “kératos”=horn and “trichium”=thread) were described for the first time by Krukenberg (1880) in the fins of selachians. These rays are characteristic of the Chondrichthyes, and are present in modern and fossil elasmobranchs and holocephalans (Goodrich 1904; Dean, 1909; Zangerl, 1973, 1981; Bendix-Almgren, 1975).

The ceratotrichia are long, cylindrical, fibrous rays that are flexible, translucent, non-segmented, and rarely branched. The proximal end is pointed and the rays gradually diminish their diameter towards the distal tip. Like actinotrichia, ceratotrichia are not derived from bone (i.e., “horny” rays) and, like all dermal rays, they are found in paired and median fins. The numerous ceratotrichia are distributed in two layers over the fins and overlap the cartilaginous radials of chondrichthyans. Placoid scales cover most of the external surface of the fins, reducing the fin web to a very narrow distal fringe devoid of scales.

The ceratotrichia are formed by giant fibres of collagen (elastoidin), which develop in bilateral rows within the dermis (Kemp, 1977). They grow by apposition of collagen fibrils from the peritrichial matrix (Kemp, 1977). Indeed, a layer of peritrichial fibroblasts containing secretory vesicles surrounds each ceratotrichium (Arratia et al., 2001). According to Bouvet (1974), Kemp (1977), Géraudie and Meunier (1980) and Durán et al., (2011), ceratotrichia would be homologous to actinotrichia since their development, structural and molecular components are almost identical. Actinotrichia and ceratotrichia may only be different in size. Ceratotrichia may thus represent the primitive condition from which actinotrichia evolved in osteichthyans. In turn, the presence of ceratotrichia (chondrichthyans) and/or actinotrichia (osteichthyans) is the primitive condition in the evolution of fin rays in gnathostomes (i.e., jawed vertebrates; Goodrich, 1904).

Dermal fin rays of the Placodermi have been traditionally called ceratotrichia. These rays are relatively large, three-dimensional fibrous structures that are surprinsingly frequently preserved in fossil specimens, and have been identified next to the radial bones in the pectoral fins of bothriolepis (Long, 1983), dunkleosteids (Carr et al., 2010) and stensionellids (Denison, 1978). Ceratotrichia have also been described in the two dorsal and caudal fins of *Bothriolepis* (Stensiö, 1959; Denison, 1978). In more primitive forms, the fins are distally covered by scales or tesserae.

**Dermotrichia**

The term dermotrichia (from the Greek “dermos”=dermal and “trichium”=thread) was originally used by Goodrich (1904) to describe, in a general manner, all the dermal fin rays of mesodermic (dermal) origin in vertebrates. Some authors have used it to name the fin rays of “acanthodians” (Miles, 1970; Zidek, 1975; 1976; Arratia et al., 2001). Moreover, certain

authors also refer to the fin rays of placoderms as dermotrichia (Denison, 1978). Nonetheless, Reis (1896), Watson (1937) and Heyler (1962) call the acanthodian rays ceratotrichia.

"Acanthodians" possess dermal fin rays with an ossified proximal portion and a distal, non ossified portion. According to Géraudie and Meunier (1980), this distal, non-ossified region could correspond to large actinotrichia. Proximal ossification would occur by resorbtion of actinotrichia within the skeletal tissue (see above). Friedman and Brazeau (2010) reported that in the caudal lobe of some "acanthodians" the scale rows are arrayed in a pattern that is similar to that of the lepidotrichia of sarcopterygians and actinopterygians (Heyler, 1969; Long, 1986). If both scales and lepidotrichia are, as stated above, mere "morphological manifestations of the same morphogenetic system" (Schaeffer, 1977), this may support that the proximal ossified tissue could be of a pre-lepidotrichia nature.

Early gnathostome ceratotrichia *sensu stricto* are not segmented, totally devoid of bone and never mineralize. Moreover, no distinct lepidotrichia occur in "acanthodians". Therefore, the term dermotrichia *sensu lato* would better suit to describe "acanthodian" rays. In any case, Géraudie and Meunier (1980) have warned that further fine paleohistological studies on "acanthodians" would be needed to test these hypotheses. Anyhow, all these data would confirm that actinotrichia are a primitive character for osteichthyans, originating probably in the Teleostomi (i.e., total group Osteichthyes including *Acanthodes* + stem and crown group osteichthyans, *sensu* Friedman and Brazeau, 2010).

**General considerations**

It is always difficult to count precisely the number of fin rays in fossil specimens. This is obvious when small numerous procurrent rays are considered. In neontological forms, the number of fin rays is also variable within one species (e.g., the zebrafish *Danio rerio*; Kimmel et al., 1995; Bird & Mabee, 2003). In this review, we will thus focus on the morphological

diversity of the fin rays rather than on their number. The main aim of this study is to describe the fin rays under a qualitative rather than quantitative approach. Nonetheless, quantitative data will be provided when needed.

## SARCOPTERYGII (Jorge MONDÉJAR-FERNÁNDEZ)

Sarcopterygii (from the Greek "sarx"=flesh and "pteryx"=fin or wing) comprise the so-called lobe finned fishes and the tetrapods. Among other cranial and histological features (see Cloutier and Ahlberg, 1996; Friedman and Brazeau, 2010, and references therein), sarcopterygian fishes are mainly characterized by the monobasal articulation of their paired fins. This is formed by a single articulated element (the humerus for the pectoral fin and the femur for the pelvic fin) located between the fin endoskeleton and the girdle. Besides, muscles are well developed at the base of these fins (e.g., Millot and Anthony, 1958). Thus, sarcopterygians owe their name to their fleshy lobed fins.

Sarcopterygians were highly diversified during the Devonian, but only three groups survive today: the actinistians (one genera, *Latimeria*, with two species), the dipnoans (three genera, *Neoceratodus*, *Lepidosiren* and *Protopterus*, with six species), and the tetrapods (approximately 30 000 species) (Lecointre & Le Guyader, 2001). Classically, Sarcopterygii class has been considered to comprise seven orders, most of them of doubtful monophyly: Onychodontida, Actinistia, Porolepiformes, Dipnoi, Rhizodontida, Osteolepiformes, Elpistostegalia and Tetrapoda (Janvier, 1996) (considerations on the monophyly of these groups will be presented later). However, the broad phylogenetic framework of sarcopterygians comprise two large monophyletic groups: the Dipnomorpha (comprising the dipnoans and their closest relatives, the Porolepiformes), and the Tetrapodomorpha (comprising all sarcopterygians more related to tetrapods than to dipnoans; Ahlberg, 1991).

Both groups are gathered under the clade Rhipidistia (Cloutier & Ahlberg, 1996; Janvier, 1996). The Onychodontida and the Actinistia lie outside the Rhipidistia. Nonetheless, their interrelationships and relationships to rhipidistians are still debated (e.g., Cloutier & Ahlberg, 1996; Zhu & Schultze, 1997; Lu & Zhu, 2010).

Sarcopterygian fishes show a rather stable fin pattern in all groups. There are always two sets of paired fins: two pectoral fins located behind the head, and two pelvic fins located at the level or between the dorsal fins. The median fin pattern comprises generally two dorsal fins, one anal fin and one caudal fin. The dorsal and anal fins can be lost or modified in certain derived lineages (see below). The caudal fin is supposed to be primitively heterocercal but tends to become diphycercal in almost all lineages. Each fin is composed of a basal endoskeleton and a distal dermoskeleton. The dermal skeleton is primitively composed of lepidotrichia (except in derived dipnoans with camptotrichia, see below) which are generally segmented, branched, articulated with the endoskeleton skeleton, and distally tapered to actinotrichia bundles.

Early representatives of the Sarcopterygii include the Chinese forms *Meemania*, *Psarolepis, Achoania* and *Styloichthys* (Yu, 1998; Zhu and Yu, 2002; Zhu et al., 1999, 2001, 2006). These Early Devonian taxa are considered as stem sarcopterygians and do not fit in any broad, formerly defined sarcopterygian group (with the possible exception of *Styloichthys*, see below). Unfortunately, the fins are not preserved in any of these early forms (except in *Psarolepis* and *Styloichthys* for which several bones of the shoulder girdle are known). Hence, fin ray structure remains largely unknown in these stem sarcopterygians.

However, certain general inferences can be made through comparison between osseous fin rays and scales. In *Meemania*, the dermal bones of the skull present a primitive type of cosmine in which the pore-canal network is associated with a series of superimposed enamel-dentine couplets (Zhu et al., 2006, 2010). In more derived sarcopterygians (see

below), a single enamel-dentine layer is formed. Since cosmine, when present in sarcopterygians, is found in both scales and lepidotrichia (e.g., cosmine covered porolepiforms, dipnoans, and "osteolepiforms"; Ørvig, 1957, Denison, 1968a,b; Jarvik, 1959, 1980; Mondéjar-Fernández and Clément, 2012), we can infer that the lepidotrichia of these early sarcopterygians must have had a cosmine covering, identical to that present in the dermal scales. Nevertheless, no inference on segmentation and bifurcation patterns of the lepidotrichia in these basal sarcopterygians can be obtained from the literature. The earliest evidences of lepidotrichia are found in the Silurian stem sarcopterygian *Guiyu* (Zhu et al., 2012a) and in Early Devonian dipnoans and porolepiforms (see below).

Herein, we will present the main groups of sarcopterygians (after the phylogenetic classification in Janvier, 1996). Each group review will comprise a short introduction about their distribution and phylogenetic interrelationships, an overall description of their fin pattern, and a thorough description of the fin rays structure and arrangement. For those groups with extant representatives (e.g., actinistians and dipnoans), we will separate the fossil description from that of the extant taxa in order to set a detailed extant framework and to facilitate comparisons.

**Stem Sarcopterygii**

The stem sarcopterygians herein described correspond to recently discovered new fossil taxa that cannot be confidently attributed to any of the formerly presented sarcopterygian groups. These new forms include puzzling fishes from the Late Silurian and Early Devonian of China such as *Psarolepis romeri* Yu, 1998*, Achoania jarvikii* Zhu et al., 2001*, Styloichthys changae* Zhu & Yu, 2002*, Meemannia eos* Zhu et al., 2006*,* and *Guiyu oneiros* Zhu et al., 2009. Their phylogenetic position is still debated; *Psarolepis* was formerly

considered a dipnomorph (Yu, 1998) but now it is generally placed along the stem Sarcopterygii (Zhu et al., 1999, 2001; Zhu & Yu, 2002), *Styloichthys* was considered the sister group of rhipidistian (Zhu & Yu, 2002) but has recently been considered a putative basal actinistian (Friedman, 2007), and *Guiyu* could possibly be a basal sarcopterygian (Zhu et al., 2009) but lacks cosmine and show a set of primitive features in its scales that would exclude it from the osteichthyan crown group (Friedman & Brazeau, 2010). *Meemannia* and *Achoania* are generally located as successive sister groups of onychodontids and actinistians along with *Psarolepis* (Zhu et al., 2006).

For most of these forms the postcranial anatomy is still unknown. *Meemannia* and *Achoania* are solely represented by cranial material (Zhu et al., 2001; 2006). *Styloichthys* and *Psarolepis* are known from articulated cranial and disarticulated postracranial material, mostly pectoral girdles (for *Styloichthys*) (Zhu & Yu, 2002) and pelvic girdles (for *Psarolepis*) (Zhu et al., 2012a). *Guiyu* is the most completely preserved (Zhu et al., 2009, 2012a), and although the caudal fin shape is still hypothetic, the median fin pattern is representative of the primitive condition in osteichthyans, and more particularly in sarcopterygians.

*Guiyu* possess two dorsal fins and an anal fin located posteriorly to the second dorsal fin. Both dorsal fins show a bony median fin spine on the trailing edge, as in *Psarolepis* (Zhu et al., 1999). No fin spine is found for the pelvic and anal fins. Lepidotrichia are partially preserved in the pectoral, second dorsal and anal fin of the *Guiyu* holotype (Zhu et al., 2012a). They are segmented and, certainly, covered by a ganoine-like enamel, as in the scales.

**Onychodontida**

The Onychodontida ("Struniiformes" or Onychodontiformes) are an enigmatic stem sarcopterygian group of which affinities within the Sarcopterygii are disputed (e.g., Panchen & Smithson 1987; Zhu & Schultze 2001; Long 2001). Onychodontids were marine eel-like predatory fishes of variable size occurring worldwide from the Early Devonian (Pragian) to the Late Devonian (Famennian). They are currently represented by six genera: *Bukanodus* Johanson et al., 2007; *Grossius* Schultze, 1973; *Lukeus* Young & Schultze, 2005; *Onychodus* Newberry, 1857; *Qingmenodus* Lu & Zhu, 2010 and *Strunius* Jessen, 1966.

It is widely recognized that the Onychodontida are a monophyletic group (Cloutier & Ahlberg 1996; Janvier 1996; Andrews et al. 2006; Campbell & Barwick 2006; *contra* Friedman 2007; Lu & Zhu 2010). For other phylogenetic considerations see Schultze (1987); Long (1989, 2001); Young et al. (1992); Cloutier & Ahlberg (1996); Zhu & Schultze (1997, 2001); Lu & Zhu (2010) and Zhu et al. (1999, 2001, 2006).

Our knowledge on onychodontids morphology is mostly based on disarticulated and fragmentary skull material, the endoskeleton being poorly known. The best known onychodontids are *Onychodus jandemarrai* from the Frasnian of Gogo, Western Australia (Andrews et al. 2006) and *Strunius walteri* from the Frasnian of Bergisch-Gladbach, Germany (Jessen, 1966). The oldest onychodontid is *Bukkanodus jesseni* from the Pragian of Victoria, Australia (Johanson et al., 2007), which is also the sister taxon of other onychodontids (Lu & Zhu, 2010), but unfortunately it is solely known from disarticulated and fragmentary skull material.

The paired fins of onychodontids are poorly known. They are only preserved in its entirety in *Strunius* where they are small, triangular in shape and of similar size between the pectoral and the pelvic fin (Jessen, 1966). In *Strunius,* the pectoral fin is displaced further

back by a posteriorly elongate ventral lamina of the cleithrum and seems to be located more ventrally than in other sarcopterygians. The pelvic fin is located at the level of the first dorsal fin.

The median fin pattern is constant in onychodontids for which fins are preserved and shows the classical sarcopterygian condition, with two dorsal fins. The caudal fin is diphycercal in *Strunius* and *Onychodus*.

Since only two genera of onychodontids are known in substantial anatomical detail, the differences in shape and structure of the fins and fin rays will be detailed for *Strunius* and *Onychodus* separately.

In *Strunius walteri* (Jessen, 1966, fig.7), the pectoral and pelvic fins are both short and very similarly shaped (see above). There are two dorsal fins, the anterior being somewhat smaller than the posterior one. The size of the anal fin is equal size to that of the second dorsal fin and lies slightly posterior to the latter. The caudal fin is diphycercal with large upper and lower lobes that are symmetrically arranged, and presents a long axial (middle) lobe. The lobe alone forms half the length of the entire caudal fin. The shape and length of the axial lobe could correspond to a juvenile character in *Strunius* (see discussion). The dorsal fins and the epichordal lobe of the caudal fin appear to be of similar size.

Jessen (1966) described the dermal fin rays (lepidotrichia) of *Strunius* as unsegmented and distally branched in all fins, except in the long middle lobe of the caudal fin, where they are short and unbranched. The branching occurs in the most distal part of the ray, near the fin fringe. The proximal-most portion of the rays is overlapped by the body scales in the dorsal and ventral lobes of the caudal fin where they articulated very likely with a series of hidden radials.

In *Onychodus jandemarrai* (Andrews et al., 2006, fig.62-66), the paired fins are poorly known and their general shape is unknown. The pectoral fin is solely represented by the

humerus and the pectoral girdle. The pelvic fin is broadly based and no supporting radials are known. The lepidotrichia are pointed in their proximal end, externally rounded at the distal one and grooved on their internal surface. This is a classical condition in sarcopterygians like *Holoptychius* and *Eusthenopteron* (see Jarvik, 1959, 1980; Zylberberg et al., 2010).

In the first dorsal fin, no endoskeletal fin support structures (radials) are known and they appear to be absent; the lepidotrichia articulate directly with the basal plate. This pattern is also known in the first dorsal fins of the porolepiform *Glyptolepis* (Ahlberg, 1991) and the coelacanth *Latimeria* (Millot & Anthony, 1958). The lepidotrichia are short and stiff in their proximal unsegmented region and they are segmented and branched in their distal region. The branching occurs shortly after the emergence of the lepidotrichia from the scale covering, thus near the base of the ray. In the second dorsal fin the lepidotrichia overlap a series of four radials. The lepidotrichia are pointed at their proximal ends and show very thick walls. As in the first dorsal fin, they are segmented and distally branched.

The anal fin is incompletely known. The shape of the fin cannot be determined accurately due to the incompleteness of the fossil specimen. No radials are preserved, however the overall morphology and lepidotrichial structure can be assumed to be very similar to that of the second dorsal fin.

The diphycercal caudal fin shows two nearly symmetrical diamond-shaped dorsal and ventral lobes and a short axial middle lobe, slightly turned upwards. The lepidotrichia are fine and numerous. The unsegmented proximal region of the rays has long and pointed ends, with a slight furrow on the medial surface. A very narrow margin of the lepidotrichia, distal to the scale covering, shows fine segments and branches. The lepidotrichia increase in length from anterior to the posterior in both the dorsal and ventral lobes of the caudal fin. Each caudal radial must have supported four lepidotrichia (Andrews et al., 2006).

In summary, we can say that in onychodontids, the lepidotrichia pattern of segmentation and bifurcation is variable, ranging from unsegmented but branched lepidotrichia in *Strunius* (Jessen, 1966) to segmented and branched, variably-sized lepidotrichia in *Onychodus* (Andrews et al., 2006). This morphological heterogeneity, especially in *Strunius*, is at odds with the archetypical pattern of segmented and/or branched lepidotrichia seen in other sarcopterygians and actinopterygians. In these groups, bifurcation mostly occurs in segmented rays, but not the contrary (see discussion). This strange pattern could be better assessed with the discovery of more complete onychodont postcranial and fin material.

**Actinistia**

The Actinistia, or coelacanths *sensu lato*, are one of the most emblematic groups of lobe-finned fishes. Coelacanths have a long evolutionary history, from the Middle Paleozoic to Recent, comprising nearly 50 fossil genera worldwide (Cloutier & Forey, 1991; Forey, 1998). Indeed, they show a very diverse range of sizes and modes of life, from shallow marine and lacustrine environments during the Palaeozoic (Cloutier, 1996) and Mesozoic (Poyato-Ariza et al., 1998), to the deep marine habitat of the extant coelacanth *Latimeria* (Fricke et al., 1987). They reach their maximum taxonomic diversity during the Lower Triassic (Cloutier & Forey, 1991), however the greatest morphological disparity occurs in the Devonian and the Carboniferous.

Our knowledge of early Devonian forms has been greatly enhanced in the past years with the discovery and redescription of some morphologically and phylogenetically important taxa, such as *Shoshonia arctopteryx* (Friedman et al., 2007), *Holopterygius nudus* (Friedman & Coates, 2006), *Miguashaia bureaui* (Cloutier, 1996), and the putative actinistian

*Styloichthys changae* (Zhu & Yu, 2002; Friedman, 2007). The extant coelacanth *Latimeria chalumnae* has given the living landmark from which all descriptions of fossil taxa and comparisons are made (Millot & Anthony, 1958; Forey, 1998). *Eoactinistia foreyi* from the Lower Devonian (Pragian) of Australia is considered as the oldest actinistian (Johanson et al., 2006), although it is only known from a dentary bone. *Miguashaia bureaui*, a well-preserved Late Devonian (Frasnian) coelacanth from Québec (Cloutier, 1996a), is considered as the plesiomorphic sister taxon to all other coelacanths.

The postcranial skeleton of coelacanths is well known and is considered as derived amongst osteichthyans. It used to be described as conservative in structure throughout the evolutionary history of the group (Forey, 1998). However, new studies and reassessments of fossil Palaeozoic actinistians (e.g., *Allenypterus, Shoshonia,* and *Holopterygius*) are at odds with this apparent morphological "stability" (Friedman & Coates, 2006; Friedman et al., 2007). Early actinistians show high levels of morphological disparity. Due to their long evolutionary history and relatively rich fossil record, the amount of data concerning the postcranial and dermal skeleton of actinistians is quite overwhelming among sarcopterygians. Herein we will first describe the general fin pattern of fossil and extant actinistians *inter alia*. We will briefly review the main characteristic of the fins and rays of the extant *Latimeria* in order to better asses and, finally describe, the morphological diversity of the fin rays in fossil coelacanths.

The paired fins of actinistians are single-axis fins, representing the primitive condition for sarcopterygians (Forey, 1998). The endoskeleton is composed of four large axial mesomeres. In the pectoral fin, the endoskeleton is slightly longer in than the pelvic fin. The lepidotrichia are arranged around the tip of the fin, with the longest rays being the medial ones. Both the leading preaxial and postaxial lepidotrichia are associated with the radials,

attached to the fourth mesomeres in *Latimeria,* but in some fossil taxa the lepidotrichia can articulate with more proximal mesomeres.

The median fin pattern of actinistians shows the classical sarcopterygian condition, with two dorsal fins and a characteristic trilobated caudal fin, similar to that of onychodontids (see above) but unique to coelacanths among extant fishes. The anterior dorsal fin is located well anteriorly, usually within the anterior half of the body, a condition different from that in other lobe-finned fishes. The lepidotrichia are supported by a plate-like basal bone strengthened by thickened ridges. The second dorsal fin is also located relatively more anteriorly than in other sarcopterygians and lies opposite, or nearly opposite, to the anal fin. The second dorsal and anal fins are each supported by a single basal plate that shows a unique and more complex arrangement than that of other sarcopterygians. In these lobate fins the lepidotrichia articulate with a single axis composed of a least four endoskeletal mesomeres, which are extremely similar to those forming the axis of the paired fins (Forey, 1998). This condition is characteristic of coelacanths and unique to *Latimeria* among extant fishes. As in the paired fins, the lepidotrichia in all lobate median fins are inserted almost symmetrically around the tip of the fin axis.

The caudal fin is composed of three lobes (upper, middle and lower lobes) and therefore it is described as trilobate, except in *Miguashaia* (Cloutier, 1996a), which has a heterocercal tail. In most coelacanths, the upper (epichordal) and lower (hypochordal) lobes are approximately equal in size and carry the same number of lepidotrichia. Nevertheless, in many fossil taxa there is a slight asymmetry in the numbers of caudal lepidotrichia and internal radial supports between the lobes. In the latter taxa, the dorsal lobe is usually longer than the ventral one. This condition is considered as an apomorphy of coelacanths with trilobate diphycercal fins above *Miguashaia* (Cloutier, 1996a). The supplementary lobe is also a derived feature of coelacanths above *Miguashaia* and it shows a symmetrical arrangement

of fin rays around the terminal end of the notochord. This lobe is always separated from the upper and lower lobes and there is a clear gap between the dermal fin rays of the principal caudal lobes and the fin rays within the supplementary axial lobe (Forey, 1998). The precise function of the axial lobe remains unknown but it is most probably used during the singular locomotion of coelacanths (Fricke et al., 1987). Millot and Anthony (1958) postulated that this supplementary lobe could be able to regenerate in *Latimeria*.

***Latimeria***

In the extant coelacanth *Latimeria chalumnae,* the median and paired fin structure has been well studied by Millot and Anthony (1958) so that an abbreviate description will be presented here.

In the pectoral fin, the lepidotrichia form a series of 32 or 33 rays. The lepidotrichia are segmented, the joints being less spaced towards the distal end of the rays. The length of the lepidotrichia increases towards the fin axis, and then diminishes gradually. The rays are stout at their base but become flat, more flexible, and distally segmented, at the level of the insertion line of the skin. The lepidotrichia overlay the radials, more broadly in the preaxial side of the fins than in the postaxial one.

In the pelvic fin, there are 36 segmented lepidotrichia. The proximal portion of the rays is overlapped by the scales and is not segmented. The exposed distal portion is segmented and is ornamented by denticles on its external surface.

In the first dorsal fin, there are 8 large and stout lepidotrichia, segmented in their most distal part. The lateral sides of the rays show an arrangement of dentine-made odontodes with a coating of enamel that are considered homologous with the tubercles of fin rays of *Lepisosteus* (Goodrich, 1904). The anteriormost rays are segmented in their distal third, whereas in the posteriormost ones, the segmented region reaches half of the ray length; thus,

the point of origin of segmentation seems to become more proximal from the anterior to the posterior region of the first dorsal fin.

The second dorsal and anal fins bear 32 lepidotrichia each. The fins are almost mirror images of each other and the fins rays are arranged and articulate with the mesomeres in both fins in the same manner (see above). The lepidotrichia are segmented with a similar pattern in each fin, the segmentation point becoming more proximal in the posterior part of the fin.

The caudal fin carries 44 fin rays, with the dorsal and ventral lobes showing 22 rays each. The lepidotrichia are segmented but unbranched in *Latimeria* and have a 1:1 ratio with the supporting radials. The unsegmented proximal region of the fins is covered by scales. The lepidotrichia show the same characteristic odontode ornamentation as those of the other fins. The segmentation and denticle ornamentation of the rays initiates distal to the scale-overlapped area. However, their segmentation is irregular; some rays can be incompletely or entirely segmented along their length while others are not, and no clear pattern is identified (Arratia et al., 2001). The middle supplementary lobe carries 30 to 35 short segmented lepidotrichia ornamented with denticles. The rays are small, thin, and usually incompletely ossified. They do not articulate with the osseous radials but with the basidorsal and basiventral elements of the vertebral column (Arratia et al., 2001).

Géraudie and Meunier (1980) identified the presence of actinotrichia in the distal end of the lepidotrichia of the second dorsal fin of *Latimeria*. In this fin, the fine structure of the coelacanth actinotrichia is identical to that of actinopterygians (e.g., teleosts). This enables to consider the presence of actinotrichia in extant actinopterygians and sarcopterygians as a plesiomorphic character for osteichthyans. Actinotrichia are likely present in all other fins of *Latimeria*, but no thorough study has been done on this topic.

**Fossil actinistians**

In fossil actinistians, the arrangement and structure of the lepidotrichia are similar to that of the extant *Latimeria*. However, there is a large variability in the number of rays, ornamentation, segmentation, and bifurcation patterns.

In the pectoral fin of *Latimeria,* the fin rays are symmetrically arranged like a fan around the tip of the fin (Millot & Anthony, 1958; Forey, 1998) with the lepidotrichia articulating with the fin mesomeres. However, in fossil coelacanths, such as the Devonian *Shoshonia* (Friedman et al., 2007, fig.1) and the Triassic *Laugia* (Forey, 1998, fig. 11.10) the insertion span of the lepidotrichia differs in preaxial and postaxial sides of the fin. The anterior (preaxial) rays are longer than the posterior (postaxial) ones, and they extend much further forward along the fin than those on the posterior margin. Asymmetrically arranged lepidotrichia seem to be a primitive character in coelacanths and could be related to the incompletely ossified distal portion of the paired fin endoskeleton (Forey, 1998; Friedman et al., 2007) and therefore symmetrical ray insertion and disposition around the fin are derived characters within the group. Cloutier (1996) reported that a few pectoral fin rays of the primitive actinistian *Miguashaia* are distally branched.

In the pelvic fin, the lepidotrichia are usually slender in fossil coelacanths. However, some taxa may have expanded pelvic lepidotrichia as in *Lybis*, where all other fin rays are also expanded (Forey, 1998). Forey (1998) pointed out that expanded pelvic fin lepidotrichia would be a feature of maturity or a difference between the sexes based on a survey on the well known Triassic form *Laugia.* Besides that, the structure of the paired fin rays, as already described for *Latimeria,* is conservative in all known fossil actinistians.

The anterior dorsal fin can carry up to 20 rays in fossil coelacanths; e.g., 10 in *Hadronector* (Lund & Lund, 1985) and *Holophagus* (Forey, 1998), 12 in *Coelacanthus* (Forey, 1991; 1998), around 15 in *Allenypterus* (Lund & Lund, 1985) and *Holopterygius*

(Friedman & Coates, 2006), and around 18 in *Miguashaia* (Cloutier, 1996). Along with the extant *Latimeria*, the Mesozoic coelacanths *Piveteauia* (Clément, 1999)*, Whiteia*, and *Macropoma* (Forey, 1998) display the smallest numbers of first dorsal fin rays among actinistians (between 6 and 8). However, all the lepidotrichia of the first dorsal fin are segmented. It is not clear whether the first dorsal fin rays of *Miguashia* are distally branched or not (Cloutier, 1996a).

The second dorsal fin of all coelacanths is more or less lobated (Forey, 1998) except for *Miguashaia* (Cloutier, 1996a) and *Allenypterus* (Lund & Lund, 1985). The insertion of the fin rays is variable, ranging from a symmetrical arrangement in *Macropomoides*, *Undina* and *Holophagus,* to an asymmetrical one in *Laugia*, *Caridosuctor* and *Rhabdoderma* (see Forey, 1991). As in the first dorsal fin, all the lepidotrichia of the second dorsal fin are segmented. Only the Devonian form *Miguashaia* show segmented and distally branched dorsal and anal fin rays (Schultze, 1973; Cloutier, 1996a) beginning from the fifth ray. The distal bifurcation of the lepidotrichia is no longer present in more derived actinistians. Branched dorsal fin rays thus seem to be the primitive condition for coelacanths.

The anal fin is almost identical in structure and morphology to the second dorsal fin. Therefore, the distribution, insertion, and structure of the lepidotrichia are similar to those in the second dorsal fin for all known taxa. The basic structure of the second dorsal and anal fins seems to have remained unchanged since the early evolutionary history of the group.

The caudal fin is probably the most variable one regarding shape, structure, and fin ray distribution. The tail of *Miguashaia* is heterocercal with a well-developed ventral lobe, a narrow dorsal lobe, and lacks the characteristic axial lobe. This morphology likely corresponds to the primitive condition, not only of actinistians, but also of sarcopterygians as a whole. In more derived coelacanths the caudal fin is composed of three lobes (as in *Latimeria*) with the dorsal lobe usually carrying more rays than the ventral one. The tail can

be relatively elongated as in *Coelacanthus* and *Laugia,* or short as in *Macropomoides, Axelrodichthys* and *Holophagus* (see Forey, 1998). However, the most striking tail morphology is the asymmetric, ribbon-like caudal fin of *Holopterygius* and *Allenypterus* (Lund & Lund, 1985; Friedman & Coates, 2006). This fin shows a dorsal lobe that extends far anteriorly, occupying the posterior half of the body. The ventral lobe in *Allenypterus* is reduced to a small series of fine lepidotrichia in the most posterior region of the tail (Friedman & Coates, 2006), whereas in *Holopterygius* it is more extensive, spreads anteriorly, and is nearly symmetrical to the dorsal lobe. The recently discovered coelacanth *Rebellatrix* from the Triassic of Western Canada shows a fork-tailed caudal fin (Wendruff & Wilson, 2012).

The axial lobe varies in length in fossil taxa, both between adults of different species and during the ontogeny (Forey, 1998). As in other sarcopterygians, the axial lobe is longer in juveniles than in adults (see discussion). It is rarely preserved intact in fossil specimens and therefore its total length is difficult to measure. As in *Latimeria*, the lepidotrichia of this lobe do not articulate with endoskeletal radials in fossil actinistians.

The lepidotrichia are normally distally segmented but unbranched in the caudal fin, except in *Allenypterus* (Lund & Lund, 1985) and probably in *Holopterygius* (Friedman et al., 2007) where the fin rays of the ventral caudal lobe are neither segmented nor branched, and in *Diplocercides heiligenstockensis* where Jessen (1973; fig. 3b) illustrated a single bifurcated lepidotrichium in the caudal fin. Actinistians usually show an equal number of fin rays and supporting radials. However, once again, only *Miguashaia* shows not only a higher number of fin rays than radials in the tail, but also presents branched lepidotrichia in the caudal fin (Schultze, 1973; Cloutier, 1996a). The lepidotrichia of the dorsal (epichordal) lobe are short and the most distal ones are branched, whereas those of the anterior ventral (hypochordal) lobe are long and branched along the entire lobe (Cloutier, 1996a). A greater than one-to-one

relationship between fin rays and radials is also known in the Palaeozoic forms *Holopterygius* (Friedman et al., 2007), *Allenypterus* (Lund & Lund, 1985), *Lochmocercus* (Lund & Lund, 1984), *Nesides* (Jessen, 1973), and *Diplocercides* (Stensiö, 1922, 1937). This condition is presumed to be plesiomorphic and, as for the median fins, branched caudal fin rays seem to be primitive for actinistians.

A peculiar condition of the most elongated actinistian lepidotrichia is the presence of an anteroproximal and a posterodistal flange that articulate each segment with the following one in an imbricating pattern. Such flanges occur in the lepidotrichia of the second dorsal and anal fins and in the ventral lobe of the tail in certain fossil taxa, and would have prevented the lepidotrichia from bending. Theese flanges have been recorded in the Devonian forms *Miguashaia* (Cloutier, 1996a), *Diplocercides* (Stensiö, 1932), *Nesides* (Jessen, 1973), *Gavinia* (Long ,1999), and *Shoshonia* (Friedman et al., 2007), but are lost in post-Devonian taxa (Forey, 1998).

The odontode ornamentation of the lepidotrichia is another characteristic of derived actinistians. In the Mesozoic forms *Rhabdoderma, Piveteauia, Laugia, Coelacanthus*, *Trachymetopon*, *Chinlea*, and *Garnbegia,* none of the first dorsal fin rays bear any denticle. However, in the extant *Latimeria*, the Triassic *Whiteia* and many other Mesozoic actinistians, denticle ornamentation is present (Clément, 1999). Moreover, the Carboniferous *Hadronector* (Lund & Lund, 1985) also has ornamented fin rays. According to Forey (1991) and Cloutier (1991), unornamented lepidotrichia are primitive for actinistians. Thus, the presence of odontodes in the fin rays of *Latimeria* and other Mesozoic coelacanths is a derived feature. Their presence in *Hadronector* could be considered as an autapomorphy of the genus. However, the function of these denticles is still unknown.

In summary, the lepidotrichia in actinistians play a role as a phylogenetic character within the evolutionary history of the group. Branched lepidotrichia in the median fins is a

primitive character for actinistians, lost in derived forms above the Devonian *Miguashaia* (Cloutier, 1996a). Segmented lepidotrichia are widely spread in actinistians, however segmentation can be an ontogenetic character present only in adult forms (e.g., in juvenile specimens of *Rhabdoderma* the lepidotrichia are not segmented but they become distally segmented in adults [Arratia et al., 2001]). Ornamentation structures of the rays (e.g., odontodes, flanges) seem to be a unique characteristic of the actinistian lepidotrichia. Actinotrichia are also likely to be present in the fins of all actinistians but, due to their fibrous nature and difficult preservation in fossil specimens, they are only known in the extant *Latimeria*. Finally, as Cloutier (1996a) pointed out concerning the primitive condition of *Miguashaia*, only the segmented lepidotrichia could be branched. We confirm this assertion since we have seen that there are no unsegmented and branched lepidotrichia in actinistians.

**Porolepiformes**

The Porolepiformes are an exclusively fossil group of predatory sarcopterygians that inhabited near-shore marine and lacustrine environments from the Early Devonian (Lochkovian) to the latest Devonian (Famennian) of Euramerica. Recent evidences attest though that certain forms might have migrated to Gondwana (Johanson et al., in press; Mondéjar-Fernández et al., in press). Currently, the Porolepiformes comprise 12 genera: *Duffichthys* Ahlberg, 1992; *Glyptolepis* Miller ex Agassiz, 1841; *Hamodus* Obruchev, 1933; *Heimenia* Ørvig, 1969; *Holoptychius* Agassiz, 1839; *Laccognathus* Gross, 1941; *Nasogaluakus* Schultze, 2000; *Paraglyptolepis* Vorobyeva, 1987; *Porolepis* Woodward, 1891; *Pseudosauripterus* Ball et al., 1961; *Quebecius* Schultze, 1973; and *Ventalepis* Schultze, 1980.

Jarvik (1942) split the order Porolepiformes into two families: Porolepididae (comprising *Porolepis* and *Heimenia*), and Holoptychiidae (comprising *Holoptychius*, *Glyptolepis* and *Laccognathus,* among others). There is little morphological variation between both families. The "porolepidids" differ from the holoptychiids in having a longer anterior cranial division, a posteriorly shallow lower jaw, and a cosmine covering on their rhombic scales and dermal bones (Ahlberg, 1992b). In turn, holoptychiids present rounded scales devoid of cosmine (Ørvig, 1957; Mondéjar-Fernández & Clément, in press). .

The monophyly of the group has been well established (Cloutier and Ahlberg, 1996), however "Porolepididae" is defined mainly on plesiomorphic characters for sarcopterygians and therefore it could represent a paraphyletic assemblage of primitive porolepiforms (Maisey, 1986; Ahlberg, 1991; 1992a,b). The Porolepiformes are currently considered as the sister group of lungfishes, forming together the Dipnomorpha (Ahlberg, 1991). However, very few studies have tackled the precise phylogenetic relationships within the group. *Porolepis brevis* from the Lower Devonian (Pragian-Emsian) of Spitsbergen is the most primitive member of the Porolepiformes.

The best known genera with a well-preserved postcranial and fin skeleton are *Porolepis* (Jarvik, 1942; Clément, 2004), *Heimenia* (Clément, 2001; Mondéjar-Fernández & Clément, *in press*), *Glyptolepis* (Andrews & Westoll, 1970b; Jarvik, 1972), *Holoptychius* (Andrews & Westoll, 1970b; Cloutier & Schultze, 1996), and *Quebecius* (Schultze & Arsenault, 1987; Cloutier & Schultze, 1996). The postcranial skeleton of *Powichthys*, the putative sister group of Porolepiformes, is still unknown (Jessen, 1975; Clément & Janvier, 2004).

The paired fins of porolepiforms tend to differ in shape and size between the pectoral and the pelvic fins. The pectoral fins are long, leaf-like, nearly symmetrical, and usually narrow, with an elongate lobed middle region in all known taxa. The pelvic fins are short,

asymmetrical, usually rounded and lobate, except in *Quebecius* that shows broadly based pelvic fins (Schultze & Arsenault, 1987; Cloutier & Schultze, 1996). They are smaller than the pectoral fins and are located in the middle region of the body, anterior to the first dorsal fin. As in the leaf-like fins of dipnoans and actinistians, the lepidotrichia articulate with the radials on both preaxial and postaxial sides of the fins.

The median fin pattern, as that in other lobe-finned fishes, shows two similarly-shaped dorsal fins located in the posterior half of the body. The first dorsal fin is always slightly smaller than the second one. The second dorsal fin is usually located opposite, or somewhat posterior, to the anal fin and equal in size with the latter. According to the genera with a better-known postcranial and fin material, the main morphological differences among the dorsal fins concern the lobation of the proximal region. Fins are lobate in *Porolepis* (Clément, 2004), *Holoptychius* (Cloutier & Schultze, 1996), and *Glyptolepis* (Andrews & Westoll, 1970b; Ahlberg, 1989). *Quebecius* shows a singular dorsal, anal and pelvic fin shape with broad insertion fields (Schultze & Arsenault, 1987; Cloutier & Schultze, 1996) similar to that of *Onychodus* (see above).

The caudal fin is heterocercal in all known porolepiforms and presents a well-developed hypochordal lobe and a small epichordal lobe, except in *Porolepis* where the epichordal lobe is absent (Clément, 2004). The posterior margin of the hypochordal lobe is almost straight in *Porolepis* but more rounded and sigmoid in the more derived holoptychiids (Cloutier & Schultze, 1996; Clément, 2004). In *Porolepis* (Clément, 2004; *pers*. *obs*.), *Holoptychius* and *Quebecius* (Cloutier & Schultze, 1996), the fin rays of the ventral lobe of the caudal fin diminish in size from anterior to posterior. The same is true for the epichordal lobe in *Holoptychius* and *Quebecius*.

In the "**Porolepididae**" lepidotrichia are only known in the second dorsal and caudal fins of *Porolepis* (Clément, 2004). In contrast with the more convex limit in the lobate fins of

holoptychiids (see below), the limit between the scales and the lepidotrichia of *Porolepis* is straight across the base of the fins (Clément, 2004; pers. obs.). According to the reconstruction of the second dorsal fin of *Porolepis* by Clément (2004), the segmented lepidotrichia show numerous equally-sized segments for most of their length, except in the posterior margin of the fin where the segments become smaller. The lepidotrichia of the second dorsal fin are distally branched; the bifurcation occurs closer to the limit between the rays and the squamation in the posterior half of the fin than in the anterior one. Jarvik (1959) also reported that the lepidotrichia of *Porolepis* were grooved on the inner side, a typical condition for osteichthyans. Unfortunately, due to the type of preservation of the fossil material, the arrangement of the unsegmented region of fin rays and their relationship with the radials remain unknown.

In the **Holoptychiidae** the lepidotrichia show a more classical structure as already described. The fin rays are very numerous and slender, and they have lost the dentine and enamel covering present in the "porolepidids". Goodrich (1904) claimed that the exposed segmented region of the rays of *Glyptolepis* showed an enamel covering, however further studies (Jarvik, 1959) have failed to confirm this statement. Nonetheless, the lepidotrichia of *Glyptolepis* show a delicate ornamentation composed of fine ridges. In all other holoptychiids, this ornamentation in the external surface of the segmented portion of the rays is absent.

All known holoptychiids show segmented and distally branched lepidotrichia in all fins. The proximal unsegmented portion of the fin rays is round in cross section and particularly long, especially in *Holoptychius* (Goodrich, 1904; Jarvik, 1959, 1980; Cloutier & Schultze, 1996), covering the distal half of the supporting endoskeletal radial. The body scales in the lobate-finned holoptychiids cover the entire proximal unsegmented portion of the lepidotrichia, except in *Quebecius* where such unsegmented rays are apparent in the pelvic and all median fins and extend into the body walls (Schultze & Arsenault, 1987; Cloutier &

Schultze, 1996). Holoptychiids posses the lepidotrichia with the longest unsegmented portion among sarcopterygians (except for the extremely long unsegmented lepidotrichia of rhizodontids, see below), forming nearly the half of the ray total length in *Holoptychius*. Moreover, the branching of the distal portion of the fin rays is particularly developed in holoptychiids. For example, *Holoptychius* shows a third order branching in the lepidotrichia of its caudal and second dorsal fin (Cloutier & Schultze, 1996).

In the caudal fin of *Holoptychius* (Cloutier & Schultze, 1996) and in the pectoral fin of *Glyptolepis* (Ahlberg, 1989), each radial carries three or four lepidotrichia. Very probably a more than 1:1 ratio between radial and fin rays was present not only in holoptychiids, but certainly in all porolepiforms.

In summary, Porolepiforms may show the archetypical segmented and distally branched lepidotrichia in all their fins. The unsegmented proximal region is, however, slightly longer than in other sarcopterygians, with the exception of rhizodontids (see below). In relation to the break-up and disappearance of the cosmine in the body scales of holoptychiids, there is an interesting simultaneous loss of the cosmine in the exposed surface of the rays. This loss of the cosmine in the scales and the lepidotrichia illustrates that scales and fin rays are somewhat related in their development (Schaeffer, 1977).

**Dipnoi**

The Dipnoi, generally known as lungfishes or dipnoans, are a diverse group of sarcopterygians with a long and well documented fossil record extending from the Early Devonian (Pragian) to recent times. Dipnoans are diagnosed by the peculiar nature of their dentition formed by large tooth plates derived from palatal bones (Janvier, 1996) and a complicated cranial architecture, among other cranial characters (e.g., Cloutier & Ahlberg,

1996). There are more than 70 worldwide described fossil genera known mostly from disarticulated tooth plates. Dipnoans reached their maximum diversity during the Devonian and Triassic (Schultze, 2004) and show a progressive transition in their habitat from marine environments in the Devonian to freshwater from the Carboniferous to Recent (Long, 1993). Today they are represented by three extant genera: *Protopterus* (four species, *P. dolloi, P. annectens, P. aethiopicus,* and *P. amphibius)* from equatorial Africa, *Lepidosiren* (one species, *L. paradoxa)* from South America, and *Neoceratodus* (one species, *N. forsteri)* from Australia (Cloutier & Ahlberg, 1996; Kemp, 1986).

The monophyly of the Dipnoi has been well demonstrated; however, since the discovery of *Diabolepis* (Chang and Yu, 1984) the definition and diagnosis of the group have been debated and reformulated (Maisey, 1986; Campbell and Barwick, 1987; Panchen and Smithson, 1987; Schultze, 1987; Schultze and Campbell, 1987; Smith and Chang, 1990; Chang, 1991). Interrelationships among dipnoans have been assessed in several studies but remain highly discussed (Miles, 1977; Marshall, 1987; Campbell and Barwick, 1990; Schultze *et al,* 1993; Schultze and Marshall, 1993; Long, 1993). Attempts of classification have been made based on dentition (i.e., tooth-plated, dentine-plated, and denticulated dipnoans) (Campbell and Barwick, 1983; 1987; 1990) but currently there is no consensus concerning the phylogeny of the group.

The oldest known members of the Dipnoi are *Uranolophus wyomingensis* (Denison, 1969) and *Speonesydrion iani* (Campbell and Barwick 1983) from the Early Devonian (Pragian) from Wyoming, USA and New South Wales, Australia respectively. Other early dipnoans from the Early Devonian (Emsian) are *Sorbitorhynchus deleaskitus* (Wang *et al.* 1990) from China and *Dipnorhynchus suessmilchi* (Etheridge, 1906) from Australia. Miles (1977) considered *Uranolophus* to be the most primitive dipnoan. However, Campbell and Barwick (1984) considered this genus more derived than *Speonesydrion* and *Dipnorhynchus.*

*Diabolepis speratus* (Chang and Yu, 1984) from the early Devonian (Pragian) of Yunnan (China) is considered as the sister group of all other dipnoans. The controversial and uncertainly located *Powichthys* from the Lower-Early Devonian of Canada and Spisbergen (Jessen, 1975; Clément & Janvier, 2004) and *Youngolepis praecursor* from the early Devonian of China (Chang & Yu, 1991) represent respectively progressive sister groups of *Diabolepis* and other dipnoans. However, *Powichthys* is currently considered to be closer to porolepiforms than to dipnoans (Clément & Janvier, 2004).

Unfortunately, *Diabolepis* is of little use for comparisons on the postcranial skeleton of dipnoans since it is known exclusively from cranial material (Chang and Yu, 1984) and isolated dental elements (Smith and Chang, 1990). The oldest proper dipnoan, *Uranolophus,* is known from a single complete specimen and numerous skulls and lower jaws (Denison, 1968a, b; Campbell and Barwick, 1988). This has allowed setting the primitive pattern of the postcranial skeleton in dipnoans. *Dipterus valenciennesi* from the Middle Devonian (Eifelian-Givetian) of Scotland is the best understood representative of the early dipnoans, being known from whole bodies with well-preserved cranial and postcranial endoskeleton (Ahlberg and Trewin, 1995).

The postcranial skeleton of early dipnoans, such as *Uranolophus* or *Dipterus,* deviates slightly from the generalized sarcopterygian condition and dramatically resembles that of porolepiforms (Denison, 1968a; Campbell and Barwick, 1988; Ahlberg, 1989, 1991, 1992b; Ahlberg and Trewin, 1995). However, during the Middle to Late Devonian, new morphologies arise deriving from the primitive pattern (Ahlberg and Trewin, 1995; Cloutier, 1996b). As Friedman (2010) pointed out, postcranial anatomy can be a potential source of new characters that would help to elucidate the controversial phylogenetic interrelationships of dipnoans.

Paired fins of dipnoans are highly conservative in shape throughout most of their evolutionary history. The pectoral and pelvic fins are mirror images of each other, with the pelvic fin being always slightly smaller than the pectoral one. These fins are long, leaf-like, nearly symmetrical, and usually narrow fins, with an elongate lobed middle region, very similar to that of porolepiforms. The only exceptions are the paired fins of the extant *Lepidosiren* and *Protopterus* that show small, thin and filament-like paired fins with reduced fin rays. The lepidotrichia of the classical "leaf-like" paired fins are arranged around the tip of the fin, with both the leading preaxial and postaxial rays associated with the radials. In early forms the lepidotrichia increase in length from the proximal to the distal margin of the fin. They are unsegmented proximally and segmented and branched distally, except in *Fleurantia* where they are said to be unsegmented (Cloutier, 1996b). In the more derived forms where lepidotrichia are replaced by camptotrichia, the paired fins are of similar shape but the camptotrichia are unsegmented (e.g., *Neoceratodus* in Jarvik, 1980).

The median fins morphology is highly variable in dipnoans, especially in the early forms from the Devonian and Carboniferous. In all dipnoans the median fins lepidotrichia show a more than 1:1 ratio with the articulating radials. The same is true for the camptotrichia of more derived forms.

The median fin pattern can be divided into five broad morphotypes regardless of the arrangement of the endoskeleton elements in the fins (for a more detailed classification based on dorsal fin endoskeleton see Friedman, 2010):

**1. Independent short-based median fins, heterocercal caudal fin.**

Corresponds to the primitive condition for dipnoans (Ahlberg & Trewin, 1995) and constitutes the standard pattern for all other sarcopterygians (Andrews & Westoll, 1970b). It is known in *Dipterus* (Ahlberg & Trewin, 1995), *Soederberghia* (Ahlberg et al., 2001;

Friedman, 2010), *Rhinodipterus* (Schultze, 1975), *Rhynchodipterus* (Säve-Söderbergh, 1937), *Griphognathus* (Schultze, 1969), and *Uranolophus* (Campbell & Barwick, 1988; Long, 1989).

The dorsal fins are located in the posterior half of the body. They are separated from each other, with the first dorsal fin being smaller than the second one, a classical condition for sarcopterygians. The first dorsal fin has a narrow base and a pointed (in *Dipterus*) to rounded (in *Rhynchodipterus*) distal end. The second dorsal fin has a broader base and is more rounded than the first one, a condition similar to that of porolepiforms (see above). The anal fin is narrow-based, distally pointed, and located at the same level as the second dorsal fin. Its shape is similar to that of the second dorsal fin in *Griphognathus* and *Rhynchodipterus*, and similar to the first dorsal fin in *Dipterus*.

The caudal fin is heterocercal with a long distal projection of the notochord. Epichordal lobe is primitively absent in *Griphognathus* (Schultze, 1969), *Rhinodipterus* (Schultze, 1975), and *Rhynchodipterus* (Säve-Söderbergh, 1937), which would correspond to the primitive condition for Dipnomorphs. However, according to Ahlberg & Trewin (1995) reconstruction in *Dipterus* there is an extremely small dorsal lobe with minute unsegmented lepidotrichia located at the distal most tip of the tail. The ventral lobe, as in all other early dipnoans, is well developed with a straight ventral margin and a more or less concave posterior one formed by proximally unsegmented and distally segmented and branched lepidotrichia.

**2. Independent short-based first dorsal and anal fin, long-based second dorsal fin, heterocercal caudal fin.**

This pattern is represented by *Fleurantia* (Graham-Smith & Westoll 1937), *Pentlandia* (Friedman, 2010), *Pinnalongus* (Newman & Den Blaauwen, 2007), *Barwickia,* and *Howidipterus* (Campbell & Barwick, 2002; Long & Clement, 2009).

The first dorsal fin is narrow-based but shows a more rounded distal end than in the previous stage. The same is true for the anal fin. The second dorsal fin is greatly enlarged, showing a long base that spreads posteriorly. The lepidotrichia are unsegmented in their proximal region and segmented and branched distally in *Barwickia, Howidipterus,* and *Fleurantia*.

The caudal fin is heterocercal and shows no particular changes from the previous stage except for the development of a narrow epichordal lobe. The short epichordal lepidotrichia are unsegmented, whereas the hypochordal ones are well developed and show the classical unsegmented-segmented-branched proximo-distal pattern.

**3. Independent long-based dorsal fins, short-based anal fin, heterocercal caudal fin.**

This condition is seen in *Scaumenacia* (Jarvik, 1980; Cloutier, 1996b, 2010). The first dorsal fin is elongated but low and almost contacts the second dorsal fin. It is located more anteriorly than in the previous stages occupying the middle region of the dorsal midline of the body. The first dorsal fin support is not preserved in *Scaumenacia* and was presumably unossified. The second dorsal fin is greatly expanded, both anteriorly and posteriorly. As in *Fleurantia,* the basal plate is lost and the fin is supported by separated segmental radials. The anal fin is short-based, non-lobated, and has a basal plate carrying four radials. The lepidotrichia of the first dorsal fin are short and unsegmented whereas those of the other median fins show the classical pattern with a long unsegmented proximal region and segmented and branched distal portion (Cloutier, 1996b). As in other dipnoans all median fins lepidotrichia show a more than 1:1 ratio with the articulating radials.

The heterocercal caudal fin is dorso-ventrally narrower than in the previous stages, and shows a long distal projection of the notochord that turns upwards giving to the tail a sigmoid

shape. The lepidotrichia are short, unsegmented, and S-shaped in the epichordal lobe, and long, segmented and richly branched in the hypochordal lobe (Cloutier, 1996b).

**4. Dorsal fins incorporated into the caudal fin forming a diphycercal fin fringe with a separated short-based anal fin.**

This pattern is developed in *Phaneropleuron* (Traquair, 1871) and certain post-Devonian lungfishes below the Carboniferous *Sagenodus* (Arratia et al., 2001). The dorsal fins fuse with the dorsal lobe of the caudal fin forming a very elongated dorsal fin fringe supported by segmental radials. The dorsal lobe of the elongated caudal fin spread anteriorly and occupies more than the posterior half of the body. The axis of the caudal fin is almost horizontal resulting in a straight diphycercal caudal fin. The anal fin is separated from the other median fins and is supported by radials arising from a triangular basal plate.

**5. Dorsal, anal and caudal fin incorporated in a continuous diphycercal fin fringe.**

This condition characterizes all dipnoans from the Late Paleozoic (e.g. *Conchopoma, Uronemus, Sagenodus, Ceratodus,* and *Gosfordia* among others) to Recent (*Neoceratodus, Lepidosiren* and *Protopterus*) (Ritchie, 1981). All median fins (both dorsal and anal fins) merge with the tail fin fringe forming a diphycercal caudal fin, with the dorsal lobe extending more anteriorly than the ventral one. Lepidotrichia are absent in the fins of all Carboniferous genera above *Sagenodus* where they are fully replaced by camptotrichia. Thus the transition from lepidotrichia to camptotrichia must have occurred during the Carboniferous (see discussion).

Although it is tempting to interpret these different fin patterns as sequential steps in a transformation series, the systematics and current phylogenetic interrelationships of basal

dipnoans are not well enough resolved to support this interpretation with confidence. Moreover, it has been shown that the distribution of certain fin patterns in non-directly related dipnoan taxa imply a great degree of homoplasy in the structure of their median fins (Friedman, 2010). However, the character distribution does show that morphological change did not affect all the median fins to the same degree and at the same time (Ahlberg & Trewin, 1995). During the ontogeny of dipnoans with long-based second dorsal fins such as *Fleurantia* and *Scaumenacia* we see an anterior displacement of the anterior margin of the second dorsal fin and a posterior displacement of the anterior margin of the first dorsal fin (Cloutier, 2010). Paedomorphosis has been suggested as a primary evolutionary heterochronic process in dipnoans, mainly in relation with postcranial and fin morphology such as the fusion of the median fins, reduction of lepidotrichia, and reduction of ossification (Bemis, 1984). Based on a study on cranial ribs and their importance in air gulping during dipnoan evolution, Long (1993) proposed the hypothesis that the transition from heterocercal to diphycercal caudal fins and the incorporation of dorsal and anal fins into the caudal fin fold could have reflected the need for upward thrust from the tail to visit more regularly the water surface for air gulping in air-breathing dipnoans. However, in the absence of a fully resolved phylogeny for the Dipnoi such hypotheses cannot be confidently evaluated (Ahlberg and Trewin, 1995; Friedman, 2010).

The fin rays (i.e., lepidotrichia and/or camptotrichia) have been studied numerous times since the pioneer work of Goodrich (1904). However a great deal of confusion and erroneous interpretations have been associated with further studies principally due to the lack of a solid phylogenetic framework concerning the position of the dipnoans among vertebrates (Jarvik, 1980). Once dipnoans were firmly placed among the Sarcopterygii (Schultze, 1987) comparisons of cranial and postcranial structures with that of other sarcopterygians were more easily and usefully made. By doing so, the number of independent gains, reversions, and loss

of certain character states (e.g., cosmine) were greatly diminished resulting in more parsimonious evolutionary scenarios for the origin and evolution of the Dipnoi. The case of the fin rays falls among those characters of uncertain evolution.

The establishment of the Dipnoi as the sister group of Porolepiformes, the gathering of both groups in the Dipnomorpha, and the sister group relationship of the latter with the Tetrapodomorpha (Ahlberg, 1991) (Fig. 1) allows to apply to dipnoans the archetypical lepidotrichial pattern seen in other sarcopterygians groups and confirms that such pattern was present in the earliest members of the clade. Based on this principle is becomes possible to study the evolution of the lepidotrichia towards the camptotrichia more confidently and to identify the progressive stages of this transition.

Herein we will first describe the fin ray pattern of extant dipnoans (i.e., *Neoceratodus, Lepidosiren,* and *Protopterus*) and then compare it with the description of that of fossil taxa. Finally we will propose a morphological and histological evolutionary scenario of the transition from lepidotrichia to camptotrichia.

***Neoceratodus***

The fin rays of *Neoceratodus* are described as camptotrichia (see nomenclature). They are present in the paired fins, distributed more or less equally along pre- and postaxial sides of the pectoral and pelvic fins, and on both sides (dorsal and ventral) of the long and continuous caudal fin fold. The longest of them are located in the posterior most portion of the tail and are placed almost parallel to the axis of the body. There are no morphological differences between dorsal and ventral rays. The most posterior tip of the tail lacks rays, the vertebral column continues to the end of the caudal fin fold separating dorsal and ventral rays (Arratia et al., 2001).

In *Neoceratodus* camptotrichia are long, irregular, cylindrical rods with a tapered distal end. They are arranged in parallel and close to each other in the fin. The camptotrichia are segmented and may be branched in certain regions of the fin (Coates, 1994). The camptotrichia are not usually symmetrical on both sides of the fin and they commonly show a slight alternate distribution within the fin (Géraudie & Meunier, 1984). This condition is different to that of the symmetrical arrangement of each hemilepidotrichium in the teleost fins. The camptotrichia articulate with the most distal part of the cartilaginous or ossified radials without a one to one correlation between camptotrichia and radials (ca. 4-6 rays per radial).

In *Neoceratodus,* the camptotrichia are divided in two different parts: a superficial region formed by cellular bone, and a deep underlying unmineralized region formed by a collagen-rich tissue (Géraudie & Meunier, 1984). The proximal part of the camptotrichia is completely made of cellular bone whereas the distal tip of the ray remains unmineralized (Géraudie & Meunier, 1984). There is thus a proximo-distal gradient across the camptotrichia in which the importance of the mineralized part of the camptotrichia decreases and the unmineralized part increases inversely towards the distal tip of the ray.

***Protopterus***

The fin rays of *Protopterus* are also considered camptotrichia. They are present on both sides (dorsal and ventral) of the long and continuous caudal fin fold whereas in the paired fins they are much reduced and confined to the postaxial pectoral fin margin (Coates & Ruta, 2007). As in *Neoceratodus*, the most posterior tip of the tail lacks rays (Arratia et al., 2001). This condition is known in young and adult specimens.

The camptotrichia are simple, paired elements, completely separated from each other by the mesenchyme. Some of them articulate with the most distal part of the cartilaginous or

ossified radials. Cross sections show that they are circular throughout the ray (Géraudie & Meunier, 1984). As in other dipnoans, there is no close correlation in the number of camptotrichia and radials (ca. 4-5 rays per radial). As in *Neoceratodus* the camptotrichia are segmented and distally branched and there are no morphological differences between dorsal and ventral rays. As in *Neoceratodus* and *Lepidosiren* the last post-caudal cartilage separates both series of rays that do not reach the end of the body (Arratia et al., 2001).

In *Protopterus,* the camptotrichia are also divided in two different parts as in *Neoceratodus*: a superficial region formed by acelullar (instead of cellular in *Neoceratodus*) bone, and a deep underlying unmineralized region (Géraudie & Meunier, 1984, see above).

***Lepidosiren***

The dorsal and ventral camptotrichia are exactly as above described for *Protopterus*. However, in *Lepidosiren* camptotrichia are entirely absent from paired fins. During the breeding season, the males develop vascularised extensions in their specialised pelvic fins that can be mistaken with fin rays. The length of the rays can be very irregular in the continuous caudal fin and in certain large specimen camptotrichia show an irregular segmentation, whereas others present small, bony swellings. Camptotrichia in *Lepidosiren* are scarcely segmented and unbranched distally but some caudally located rays may show bifurcations in their proximal part (Arratia et al., 2001, Fig. 15B). *Lepidosiren* has the shortest, thinnest, softer, and less developed rays among extant dipnoans and a lower number of camptotrichia between radials (ca. 1-4 rays per radial).

Cross sections of the camptotrichia show that they are circular, completely separated from each other, and usually are regularly located, one in front the other, but separated by extensive mesenchyme. As in *Protopterus* each camptotrichium shows the more or less

developed superficial acellular bone region but it seems that the unmineralized deep portion is not continuous across the ray as in *Protopterus* (Arratia et al., 2001).

During the early stages of the ontogeny of all extant dipnoans, the continuous fin fold is supported by actinotrichia, which are later replaced by camptotrichia (Arratia et al., 2001), in the same way as actinotrichia are replaced by lepidotrichia in other osteichthyans (see above). In cross sections, Arratia et al (2001) showed that actinotrichia are not present between the camptotrichia or at their distal end, suggesting that somehow actinotrichia disappear completely during growth. Actinotrichia have neither been identified in the distal tip of the camptotrichia in adult forms, thus it seem that in dipnoans resorption of the actinotrichia during the formation of the camptotrichia is complete, as opposed to actinopterygians that retain a narrow distal fringe of actinotrichia (see above).

**Fossil dipnoans**

The fin rays of early dipnoans are considered as lepidotrichia (see nomenclature). They are present in both paired and median fins with the same arrangement as the camptotrichia of extant forms (see above).

The lepidotrichia of Devonian forms such as *Dipterus, Rhinodipterus, Griphognathus, Barwickia, Howidipterus,* and *Fleurantia,* among others (stages 1 and 2) are regularly segmented and finely branched distally. The elongate proximal portions of the lepidotrichia are round in cross section, unsegmented and their tapering proximal end articulates with the radials supporting the fin. Histological sections show that in these early dipnoans the lepidotrichia are formed by paired hemilepidotrichia developing a concave inner face towards the distal end of the ray. Among Devonian taxa, the lepidotrichia of *Uranolophus, Dipnorhynchus, Melanognathus, Dipterus, Stomiaykus, Chirodipterus, Rhinodipterus,*

*Surwepta, Ganohynchus,* and *Pinnalongus* are covered with cosmine, whereas those of *Holodipterus, Scaumenacia, Fleurantia, Griphognathus, Phaneropleuron, Rhynchodipterus, Soederberghia, Jarvikia* lack cosmine (Jarvik, 1980 and references therein). Thus the fin rays of Devonian dipnoans can be considered as representatives of the archetypical lepidotrichial pattern seen in other sarcopterygians.

As pointed above, the fins and rays of dipnoans show a well defined evolutionary trend. Middle to Late Devonian forms have independent median fins with lepidotrichia (stages 1 and 2, comprising *Dipterus, Griphognathus*, and *Fleurantia*, among others). In these forms the caudal fin shows a sigmoid to concave shape, as that of porolepiforms (see above). Moreover, the lepidotrichia of the hypochordal lobe diminish in size from anterior to posterior. Some Late Devonian forms still maintain the three separated median fins (stage 3 comprising *Scaumenacia*) but the rays of the elongate second dorsal fin and of the ventral lobe of the caudal fin are shorter than in previous stages and form a nearly parallel fin fringe with the body axis in which the fin rays are approximately equally sized. Younger forms, from Carboniferous to Recent, lose progressively the three independent fins (stages 4 and 5, comprising *Phaneropleuron*, *Conchopoma*, and extant taxa, among others) and develop a series of dorsal and ventral camptotrichia of global similar size in the continuous caudal fin. Thus it seems that the transition from lepidotrichia to camptotrichia was somewhat related to the evolution towards a uniform fin ray length in the development of the continuous tail fin fringe.

The condition of the fin rays in *Scaumenacia* deserves a special attention. Cross section of the fins shows that the proximal region of the rays is circular whereas the shape of the more distal one is flat and crescentic. Moreover, the rays lose distally their symmetrical arrangement and show a slightly alternate distribution, accentuated by the flattening of the fin during fossilization (Géraudie & Meunier, 1984, Fig. 25A). In *Scaumenacia* this peculiar

aspect of the distal fin rays could be the result of a lack of fossilization of an unmineralized internal tissue, below the mineralized external one. This morphology is strongly reminiscent of the histological structure of the camptotrichia in extant dipnoans (see above). Therefore, if we consider that the internal portion of the rays in *Scaumenacia,* was not mineralized, and consequently disappeared during fossilization, we can say that *Scaumenacia* represents the first step in the transition from lepidotrichia to camptotrichia. Moreover, *Scaumenacia* is the first Devonian dipnoan to present equidimensional fin rays in both dorsal and caudal fins (Cloutier, 1996b) thus adding a new example to support our hypothesis on related evolution between fin rays and fin morphology.

Finally we can see that in dipnoans major evolutionary transformations in fin ray structure and morphology occurred as soon as the Devonian and pursue during the Carboniferous to Recent. We list the following: (1) an important diminution of the number of dichotomies and of segments; (2) loss of the cosmine covering in the lepidotrichia; (3) homogeneity of the fin ray length in the dorsal and caudal fins; and (4) regression of the mineralization on the inner surface of the rays towards the transition from lepidotrichia to camptotrichia. This transition first evidenced in *Scaumenacia* fin rays, was inherited and spread in Late Palaeozoic and Mesozoic dipnoans to Recent (Géraudie & Meunier, 1984).

**Rhizodontida**

The Rhizodontida are a puzzling group of lobe-finned fishes that play a key role in our understanding of the radiation of tetrapodomorphs during the Devonian. Rhizodontids were very large predatory fishes (e.g., *Rhizodus hibberti* from the Lower Carboniferous of Scotland could reach up to 7 m) that inhabited in fresh water environments from the Middle-Middle Devonian (Givetian) to the Late Carboniferous (Westphalian). They are known mostly from

isolated and fragmentary skull and jaw fragments from Gondwana (Australia) and Euramerica (Scotland and United States) and are currently represented by nine genera: *Archichthys* Hancock & Athey, 1870; *Aztekia* Johanson & Ahlberg, 2001; *Barameda* Long, 1989; *Gooloogongia* Johanson & Ahlberg, 1998; *Letognathus* Brazeau, 2005; *Rhizodus* Owen, 1840; *Sauripterus* Hall, 1843; *Screbinodus* Andrews, 1985; and *Strepsodus* Huxley & Etheridge 1865.

The order Rhizodontida is considered as monophyletic (Young et al., 1992; Long, 1989; Johanson & Ahlberg, 2001). They represent the most basal Devonian radiation of tetrapodomorphs; however their phylogenetic position amongst the Tetrapodomorpha is still debated (Long, 1985, 1989; Vorobyeva & Schultze, 1991). Within the Rhizodontida, *Gooloogongia loomesi* from the Late Devonian (Frasnian) of Australia is considered as the most basal representative of the group (Johanson & Ahlberg, 2001), whereas *Aztekia mahalae* from the Middle Devonian (Givetian) of Antartica (Johanson & Ahlberg, 2001) is the oldest representative of the group, thus confirming that the group arose very probably in Gondwana.

The postcranial skeleton of the rhizodontids is poorly known. The best-known rhizodontids are *Strepsodus anculonamensis* (Andrews, 1985) from the Carboniferous of Scotland and *Gooloogongia loomesi* (Johanson & Ahlberg, 2001) from the Late Devonian of Australia for which several postcranial elements have been described. Formerly represented merely by pectoral fin remains, *Sauripterus taylori* is now known by several juvenile, nearly complete specimens (Gregory, 1935; Davis et al., 2001, 2004) from the Late Devonian (Famennian) of USA. The type material of *Strepsodus anculonamensis* could also belong to a juvenile (Andrews, 1985).

In rhizodontids, the paired fins differ in size and shape. The pectoral fins are greatly enlarged and form prominent paddles. The pelvic fins are always small, compared to the enlarged pectoral fins, and are located midway of the trunk in *Strepsodus* (Andrews, 1985) or

more posteriorly, at the level of the second dorsal fin, in *Gooloogongia* (Johanson & Ahlberg, 2001).

The median fin pattern shows the classical sarcopterygian condition, but also with remarkable differences in shape and size between the fins. There are two small dorsal fins, located in the posterior half of the body, arranged close together, and near the caudal fin. In *Strepsodus* (Andrews, 1985) the anal fin is located slightly behind the level of the second dorsal fin, whereas in *Gooloogongia* (Johanson & Ahlberg, 2001) the anal fin seems to lie anteriorly to the second dorsal fin. In all rhizodontids, the anal, first and second dorsal fins are usually small and show a rounded to slightly pointed outline.

The caudal fin shape is also variable; it can be heterocercal, as in *Gooloogongia* (Johanson & Ahlberg, 2001), or diphycercal, as in *Strepsodus* (Andrews, 1985), and probably in *Sauripterus* (Davis et al., 2001). The heterocercal caudal fin of *Gooloogongia* is composed of two well developed epichordal and hypochordal lobes unequal in size, the epichordal lobe being smaller than the hypochordal one, a condition very common among sarcopterygians, but not as reduced as that of holoptychiids or "osteolepidids" (see Jarvik, 1980). The diphycercal caudal fins of *Strepsodus* and *Sauripterus* show a rather thick axial peduncle and are posteriorly elongated with symmetrical dorsal and ventral lobes, resembling the diphycercal tail of dipnoans (see above) and Devonian tetrapods (see below).

Lepidotrichia are an important anatomical element in rhizodontids since one of the diagnostic characters of the Rhizodontida is the presence of fin rays with very long basal unsegmented segments, especially in the paired fins (Andrews & Westoll, 1970b; Andrews, 1985, Jeffery, 2001). The lepidotrichia of all the fins are stout rods of bone rounded in cross section, and unsegmented and unbranched for most of their length. Only a very narrow distal portion of the fin web shows branched and extensively segmented lepidotrichia. The unsegmented lepidotrichia of the pectoral and pelvic fins are closely crowded together, vary

in thickness, and overlie greatly many of the endochondral bones on both sides of the fin, with the preaxial lepidotrichia extending more proximally than those of the postaxial edge (Davis et al., 2001). However, in rhizodontids the overlapping of the endochondral bones by the lepidotrichia is not only restricted to the distal portion of the radials of the paired fins as in other sarcopterygians, but it extends to the "wrist" bones distal the ulna and radius in the pectoral fin (Andrews, 1985; Jeffery, 2001). Such condition is unique to rhizodontids amongst fossil and extant osteichthyans.

The proximal unsegmented region of the rhizodontid lepidotrichia is usually referred to as "basal elements" and due to their extreme robustness and enigmatic development they have been considered as non homologous to the more classical osteichthyan lepidotrichia (Johanson et al., 2005). Such elongate "basal elements" have been described and figured in *Barameda* (Long, 1989; Garvey et al., 2005; Holland et al., 2007), *Gooloogongia* (Johanson and Ahlberg, 2001), *Rhizodus* (Jeffery, 2001), *Sauripterus* (Andrews and Westoll, 1970b; Daeschler and Shubin, 1998; Davis et al., 2001, 2004), *Screbinodus* (Andrews, 1973, 1985), and *Strepsodus* (Andrews, 1973, 1985; Andrews and Westoll, 1970b; Jeffery, 2001). Some "basal segments" increasing in width towards the leading edge of the fins are present in *Strepsodus* (Andrews, 1985), *Barameda* (Long, 1989; Holland et al., 2007), and the juvenile specimens of *Sauripterus* (Davis et al., 2001). Moreover, the early ontogenetic stages of *Sauripterus* have shown that ossification of the fin dermal skeleton (i.e., fin rays) slightly preceded that of the fin endoskeleton (Davis et al., 2001). Thus in rhizodontids the endochondral skeleton did not play a particular role in fin support and locomotion until later ontogenetic stages.

Another striking characteristic of the rhizodontids is the fact that the scales of all fins overlie extensively the lepidotrichia, and cover most of the surface of the fin as in the median fins of some fossil dipnoans (Jarvik, 1959). The only visible fin web is thus reduced to the

distal-most segmented and branched portion of the lepidotrichia. This condition, combined with the elongated, unbranched proximal lepidotrichia, extends and stiffens the pectoral fin lobe into the characteristic rhizodontid fin paddle (for a functional review, see Andrews, 1985).

The condition and structure of the lepidotrichia in *Gooloogongia* is particularly interesting and sheds light on the primitive state and evolution of the fin ray structure in rhizodontids. In *Gooloogongia* only the pectoral fin lepidotrichia show the elongated "basal elements", and these only occupy about half to two-thirds the length of each lepidotrichium (Johanson & Ahlberg, 2001). By contrast, the lepidotrichia of the caudal, second dorsal and pelvic fins are segmented throughout most of their length, showing the classical osteichthyan pattern. In more derived rhizodontids such as the Carboniferous genera *Strepsodus* and *Rhizodus*, the "basal elements" constitute the majority of the ray length and are distributed in all fins (both paired and median fins) (Andrews & Westoll 1970b; Andrews 1985).

However, in *Gooloogongia* the median fins have rather short "basal elements", a condition more similar to that in "osteolepiforms" (e.g., *Eusthenopteron*), porolepiforms (e.g., *Holoptychius*) and actinopterygians. Moreover, the posterior fins of *Gooloogongia* are relatively large and are not so extensively covered by scales in their proximal region (Johanson & Ahlberg, 2001) compared to that of other more derived rhizodontids [e.g., *Strepsodus* (Andrews, 1985)]. These characters support the condition of *Gooloogongia* as the most primitive known rhizodontid (Johanson & Ahlberg, 2001) and attest that the reduction in size of the median fins and the presence of elongate and unsegmented lepidotrichia in the paired and median fins are derived characters amongst rhizodontids (Jeffery, 2001).

Another interesting issue to point out is that when the shape and structure of the fins of *Goologongia* are compared with that of more derived rhizodontids, such as *Strepsodus,* it appears that the elongation and absence of segmentation in the proximal region of the

lepidotrichia could be related in some manner with the extensive development of the scale covering of the fins, first in the paired fins and then in the median fins. Indeed, both characters are related in rhizodontids above *Gooloogongia* for which relatively well postcranial material is preserved.

Finally, we can say that in rhizodontids elongate unsegmented lepidotrichia probably first appeared in the pectoral fins (e.g., *Gooloogongia*) and then reached the pelvic and median fins in more derived forms (e.g., *Strepsodus*) thus following a classic antero-posterior axis in the spread of derived characters in fishes (see Coates, 1994). The singular occurrence of the enigmatic "basal elements" seems to be correlated with the development of an extensive scale covering, first at the base of the fin and subsequently more distally.

## "**Osteolepiformes**"

The "Osteolepiformes" are a diverse paraphyletic assemblage of Palaeozoic sarcopterygians consisting of small to relatively large predatory fishes from marine and fresh water environments. Almost 50 genera of "osteolepiforms" are known from Euramerica and Gondwana from the Middle Devonian (Eiffelian) (Cloutier, 1996c), to the Lower Permian (Sakmarian) (Schultze & Heidtke, 1986); thus representing the extinct sarcopterygian group with the greatest taxonomical diversity and the longest fossil record. However despite their large radiation during the Devonian, they show a rather conservative gross morphology.

The stretch of lobe-finned fishes considered as "osteolepiforms" has varied between studies during the last years; "Osteolepiformes" used to include all taxa more related to tetrapods than to lungfishes (i.e. the current definition of Tetrapodomorpha) (Jarvik, 1980). However today the "osteolepiform" assemblage has been narrowed and it currently comprises all extinct sarcopterygian tetrapodomorphs falling between rhizodontids and *Panderichthys*.

The “Osteolepiformes” have been traditionally subdivided in two groups: the more basal Osteolepididae, characterized by rhombic scales covered with cosmine, and the more derived, closer to tetrapods, Tristichopteridae (or disused Eusthenopteridae), characterized by rounded scales lacking cosmine (Ahlberg and Johanson, 1998). However it has been shown that scale shape and histological microstructure are no longer valid characters to distinguish unambiguously between “osteolepidids” and tristichopterids since several rhombic-scaled taxa considered as “osteolepidids”, such as *Litoptychus* may lack cosmine (Coates and Friedman, 2010). New phylogenetic studies have changed this old vision and today the paraphyletic assemblage of the “Osteolepiformes” has been split in several monophyletic families of generalized appearance such as Megalichthyidae, Canowindridae and Tristichopteridae, and some paraphyletic, uncertainly located, “Osteolepididae” such as *Gogonasus*, *Lytoptichus, Medoevia*, *Osteolepis*, and *Gyroptychius* among others (Ahlberg & Johanson, 1998; Snitting, 2008). However, the interrelationships of several groups of “osteolepiforms” basal to tristichopterids are still unresolved. Therefore we will gather all non tristichopterid “osteolepiforms” in the paraphyletic assemblage “Osteolepididae” and we will refer to those basal forms as “osteolepidids”.

“Osteolepiforms” are central in our knowledge of the fish-tetrapod transition. Many characters evolved in parallel in derived “osteolepiforms” and in tetrapods towards a morphology of large predatory fishes (Ahlberg & Johanson, 1998), and some of the main morphological transformations related to the origin of tetrapods took place in the crown ward section of the Tetrapodomorpha (i.e., “osteolepiforms” and, most particularly, tristichopterids). Despite the fact that “Osteolepiformes” is of no longer formal taxonomic value, we will use the term thereafter to gather these taxa located between rhizodontids and “elpistostegalians” in an easily discernible assemblage, knowing that the group is actually considered a grade.

The postcranial skeleton of "osteolepiforms" is one of the best known among fossil fishes thank to the numerous works of Jarvik on the tristichopterid *Eusthenopteron foordi*, the most thoroughly studied and best known fossil vertebrate (see Jarvik, 1980 and references therein). Relatively complete postcranial material is also known for *Osteolepis* (Jarvik, 1948), *Glyptopomus* (Jarvik, 1950), *Callistiopterus* (Schultze, 1973), *Canowindra* (Thomson, 1973), *Latvius* (Jessen, 1973), *Gyroptychius* (Jarvik, 1986), *Cladarosymblema* (Fox et al., 1995), *Cabonnichthys* (Ahlberg & Johanson, 1997), *Mandageria* (Johanson & Ahlberg, 1998), *Heddleichthys* (Snitting, 2009), and *Askerichthys* (Borgen, 2011).

The paired fins are rather conservative in structure and morphology among "osteolepiforms". In "osteolepidids" like *Osteolepis* and *Gyroptychius* they are rounded in overall shape (Jarvik, 1986), whereas in the more derived tristichopterids, such as *Eusthenopteron* they are more triangular and posteriorly pointed (Jarvik, 1980). The pelvic fins are slightly smaller than the pectoral ones and are usually located posteriorly, either at the level of the first dorsal fin (e.g., *Gyroptychius, Eusthenopteron*), or between the first and dorsal fins (e.g., *Osteolepis, Glyptopomus*).

The median fin pattern is highly conservative in the group; the differences between taxa rest mainly in the proportions of the body and fins. As in other sarcopterygians there are two posteriorly located dorsal fins, with the anterior dorsal fin being always smaller than the posterior one. The anal fin is of similar size as the second dorsal fin and lies opposite or slightly posterior to the latter in the ventral region.

The well developed caudal fin can be heterocercal (e.g., *Osteolepis*) or diphycercal (e.g., *Gyroptychius* and tristichopterids). There is a great diversity in the diphycercal caudal fin morphology in "osteolepiforms" where it respresents the derived condition; e.g., in *Eusthenopteron* (Jarvik, 1952) the enlargement of the middle axial lobe gives to the diphycercal caudal fin a trilobate shape, similar to that of actinistians; in *Gyroptychius* (Jarvik,

1986) the epi and hypochordal lobes are diamond shaped and almost symmetrical, whereas in *Askerichthys* (Borgen, 2011) and *Tristichopterus* (Johanson & Ahlberg, 2001), the hypochordal lobe is larger than the epichordal one. Based on a study on *Eusthenopteron*, Thomson and Hahn (1968) showed that the number of fin rays in the upper and lower lobes of the caudal fin does not change with age in "osteolepiforms". The ventral lobe of the caudal fin always contains more rays than the dorsal one, despite their similar dimensions in symmetric diphycercal tails like those of *Gyroptychius* and *Eusthenopteron*. This condition was interpreted in derived "osteolepiforms" as the last vestige of the "osteolepidid" heterocercal caudal fin. However, in "osteolepiforms" with diphycercal caudal fins there is no sign of a dorsal upturning of the distal end of the notochord as in related "osteolepidids" with heterocercal tails. The acquisition of a symmetrical caudal fin in *Gyroptychius* and tristichopterids was also inherited by more derived tetrapodomorphs (i.e., "elpistostegalians" and tetrapods, see below) and constitutes a general trend in tetrapodomorph evolution.

The lepidotrichia present the archetypical structure for osteichthyans (an unsegmented proximal portion followed by a segmented and branched distal portion) and show little variation from this uniform pattern. The fine histological structure of *Eusthenopteron*'s lepidotrichia was thoroughly studied by Zylberberg et al. (2010) and due to the current absence of further data in other taxa we will take their conclusions as the general condition for "osteolepiforms". Each fin ray is composed of two parallel hemilepidotrichia whose inner face gradually becomes concave towards the distal end of the ray and assume a crescentic shape in cross section (see nomenclature). The unsegmented proximal portion of the lepidotrichia is rounded in cross section and, as for the distal segments, exhibits concentric layers of cellular bone separated by cementing lines of arrested growth (LAGs) (Zylberberg et al., 2010). This unsegmented region of the ray is usually well developed, pointed in its proximal tip, varies in length among genera, and articulates deeply with the endoskeletal

radial, as in porolepiforms (see above) although it is slightly shorter than in the latter (Jarvik, 1959). The lepidotrichia are closely packed together and outnumber the endoskeletal radials in all fins.

Distally the lepidotrichia are uniformly segmented and branched in all fins for all known taxa. Jarvik (1959) showed than the branching occurs more frequently in the posterior rays in all fins whereas the most anterior rays, forming the leading edge of the fin, usually do not bifurcate. Jarvik (1959) also stated that tristichopterids such as *Eusthenopteron* had more richly branched lepidotrichia than "osteolepidids" but comparative data from "osteolepidids" are currently lacking to confirm or refute his assertion.

The main morphological and phylogenetic differences among the fin rays concern the ornamentation and the histological structure of the lepidotrichia. In "osteolepidids" such as *Osteolepis* and other cosmine covered forms like *Gyroptychius,* the outer exposed surface of the lepidotrichia is covered by an enamel and dentine layers showing the characteristic pore-canal system of the cosmine present in the body scales. Goodrich (1904) and Jarvik (1959) stated that the cosmine covering was restricted to the exposed portion of the fin ray and was lacking in the more proximal unsegmented portion overlapped by the fin cosmine-covered scales. To these authors the presence of cosmine in the fin rays of these forms undisputedly confirmed that lepidotrichial segments were modified scales, the entire array of lepidotrichia representing several scale rows.

On the other hand, tristichopterids like *Eusthenopteron* have lost the cosmine covering of its scales and fin rays and the lepidotrichia show a quite smooth and often somewhat shiny external surface that is most distinct from the fin and body scales. Jarvik (1959) pointed out that sometimes tubercles and other traces of scale ornamentation might be developed on the anterior lepidotrichia that are always comparatively strong and unbranched in all fins.

Early ontogenetic stages of *Eusthenopteron* from the Devonian of Miguasha (Québec) show that unsegmented lepidotrichia are present in the paired and median fins of juvenile specimens (Cote et al., 2002). Later on during ontogeny, the fin rays become segmented and bifurcated. Zylberberg et al. (2010) also showed that proximal segments adjoining to the unsegmented proximal region progressively fuse with the latter by means of mineralised, longitudinal fibres arranged in an osseous mantle at the periphery of some joints as in actinopterygians (François and Blanc, 1956).

To conclude we can say that "osteolepiforms" display a classical structure of their lepidotrichia. The homogenous branching and segmentation pattern of the rays are ontogenetic characters occurring during late stages of growth as seen in *Eusthenopteron* (Cote et al., 2002). The histological differences between the outer surface of the rays in cosmine covered "osteolepidids" and derived "osteolepiforms" lacking cosmine such as tristichopterids do not necessarily confirm that lepidotrichia are simply modified scales as proposed by Goodrich (1904) and Jarvik (1959). Moreover, the lack of cosmine in the most proximal unsegmented portion of the ray in cosmine covered "osteolepidids" like *Osteolepis* and *Gyroptychius,* among others, contradicts this scenario.

"**Elpistostegalia**"

"Elpistostegalia" or "Panderichthyida" are a paraphyletic assemblage of crown ward tetrapodomorphs, and the closest fossil relatives to tetrapods. They were large predatory fishes inhabiting the shallow waters of deltas and estuaries from Euramerica and occurring exclusively during the Late Devonian (Frasnian). Three genera are currently known: *Elpistostege* from Miguasha, Québec (Schultze & Arsenault, 1985); *Panderichthys* from

Latvia (Vorobyeva & Schultze, 1991), and *Tiktaalik* from the Ellesmere Island in the Canadian Arctic (Daeschler et al., 2006).

Before the discovery of *Tiktaalik*, Elpistostegalia was considered a clade reuniting *Elpistostege* and *Panderichthys* and diagnosed by several characters that were also present in several early tetrapods (Vorobyeva & Schultze, 1991). The position of *Tiktaalik* as the closest relative to tetrapods has broken the former monophyly of "elpistostegalians"; thus "Elpistostegalia" is currently considered a grade of crownward tetrapodomorphs, different from "osteolepiforms", and situated immediately below tetrapods (Fig. 1). However the name can also be use for the node along the tetrapod stem lineage that includes the common ancestor of *Tiktaalik*, *Panderichthys*, *Elpistostege* and tetrapods (Daeschler et al., 2006). Hereafter we will refer to this paraphyletic assemblage of finned tetrapodomorphs located at the tetrapod stem as "elpistostegalians" rather than "elpistostegalian fish".

"Elpistostegalians" share numerous characters with early Devonian tetrapods such as a long flattened skull with dorsally located eyes, the presence of ribs and the loss of the dorsal and anal fins, among other traits. However, they also retain primitive tetrapodomorph features such as a scale covering and paired fins with lepidotrichia (Daeschler et al., 2006). *Panderichthys* and *Tiktaalik* are known from relatively complete and well preserved postcranial material (Vorobyeva, 1980; Daeschler et al., 2006) whereas *Elpistostege* is solely known by an incomplete skull and several disarticulated vertebrae (Schultze, 1996). *Panderichthys* seem to be the most basal "elpistostegalian". *Tiktaalik* is the best preserved and most well known "elpistostegalian" despite the absence of a preserved caudal fin.

The paired fins of "elpistostegalians" differ from that other finned tetrapodomorphs in having an expanded endoskeleton and a relatively reduced dermal fin web. In *Panderichthys* and *Tiktaalik* pectoral and pelvic fins are located in an extreme ventral position (Vorobyeva & Schultze, 1991). The pectoral fins are relatively stouter and anteroposteriorly narrower than in

other tetrapodomorphs (Shubin et al., 2006). The pelvic fins are usually much smaller than the pectoral ones and lie well posteriorly, next to the caudal fin, occupying the level of the anal fin in other sarcopterygians (e.g., "osteolepiforms", see above). The fin web is leaf like and distally pointed with its margins running almost parallel to the external contour of the body walls.

The median fins are exclusively represented by the caudal fin; anal and dorsal fins are absent. In *Panderichthys*, the tail is diphycercal and posteriorly pointed with two symmetrical dorsal and ventral lobes, very similar to that of derived "osteolepiforms" and early tetrapods (see below). The dorsal lobe extends more anteriorly than the ventral one. The fin web surrounds the posterior end of the body completely and projects relatively further back from the distal tip of the notochord, a condition slightly different from that of "osteolepiforms" with diphycercal caudal fins like *Gyroptychius* (see above) but more similar to that of certain fossil and extant dipnoans (Arratia et al., 2001) and early tetrapods (Coates, 1996).

The lepidotrichia are segmented and distally branched in all fins. They are formed by solid rods of bone and described as rounded in cross section (Vorobyeva & Schultze, 1991; Shubin et al., 2006), however it is not clear whether they are rounded for most of the ray length or exclusively in the more proximal region, as in other sarcopterygians. Moreover, the array of lepidotrichia is not as developed as in other tetrapodomorphs (e.g., rhizodontids or "osteolepiforms"). In the pectoral fin of *Tiktaalik* the unsegmented proximal portions of the lepidotrichia articulate with the endochondral bones on both sides of the fin and overlie the distal portion of the radius, intermedium and ulnare (Shubin et al., 2006), similar to the condition seen in "osteolepiforms" and rhizodontids but not as developed as in the latter.

Lepidotrichia are more robust and articulate with the endoskeleton more proximally in the anterior (leading) edge of the fin than in the posterior one (Shubin et al., 2006). The segmented and branched region of the lepidotrichia is limited to the distal most portion of the

rays as in “osteolepiforms”. Lepidotrichia are more richly segmented and branched in the posterior margin of the fins. It has been proposed that the enhanced mobility at the level of the wrist and elbow of the well-developed distal endoskeleton in *Tiktaalik*’s fins was accompanied by an apparent reduction in the length of the distal fin rays (Shubin et al., 2006). The same must be true to *Panderichthys* (Boisvert et al., 2008). Moreover, the robustness of the paired fin lepidotrichia combined with a well developed pectoral fin endoskeleton would have allowed “elpistostegalians” to rest on the bottom of shallow water streams or even to crawl on land when needed (Shubin et al., 2006).

Finally, the structure and pattern of segmentation and bifurcation of the lepidotrichia resemble that of other tetrapodomorphs with a relatively long unsegmented proximal region and a segmented and branched distal region, the postaxial area of the fins being always more richly and proximally segmented than the preaxial one. However the length and number of the rays are reduced in “elpistostegalians”, especially in the paired fins. This condition approaches that of tetrapods, where fin rays are no longer present in the paired fins. Unfortunately we do not have enough information on the lepidotrichia of the caudal fin to compare it with that of tetrapods (see below).

**Tetrapoda**

Tetrapoda is a monophyletic group comprising all limbed vertebrates, from amphibians and reptiles to birds and mammals. Tetrapods are diagnosed by the possession of four limbs with digits, as opposed to fins with fin rays. Tetrapods are highly diverse (with around 30 000 extant species and probably more than twice as many fossil species) and occupy all kinds of habitats, from the deep seas to the airs, and from desserts to polar ice sheets. Such ecological diversity has been achieved thank to the great plasticity and

adaptability of the “chiridian” tetrapod limb responsible for the wings of bats and birds, the legs of horses, and the flippers of dolphins. The number of digits is highly variable depending on the group and shows a progressive reduction from an original polydactylous condition in Devonian forms (Coates & Clack, 1990). Anterior, posterior, or both sets of limbs can disappear in certain groups such as cetaceans (loss of the hind limbs), snakes and caecilians (loss of all limbs).

Tetrapods originate during the Middle to Late Devonian (but see Niedzwiedzki et al. (2010) for an earlier evidence of their appearance) possibly in Euramerica (Clément et al., 2004). Considering the morphological convergences observed in other large Devonian tetrapodomorphs, such as rhizodontids, tristichopterids, and “elpistostegalians” (see above) it is currently admitted that Tetrapoda arose out of one of several similar evolutionary “experiments” as large aquatic tetrapodomorph predators with reduced median fins, among other convergent characters (Ahlberg & Johanson, 1998).

The fin-limb pattern of tetrapods is characterized by the presence of digits in the paired limbs. Following Coates et al. (2002:394) definition we regard digits as “the combination of two or more spool-shaped bones/cartilages articulating one-to-one proximodistally, occurring as an anteroposteriorly arranged set or series radiating from the distal end of the limb, and bearing no simple ratio of unit-to-unit correspondence with more proximal limb parts”. These criteria are more useful to distinguish between digits and endoskeletal radials in the paired fins of derived sarcopterygians when they occur in conjunction with lepidotrichia as in rhizodontids, “osteolepiforms”, and “elpistostegalians”. Moreover, digits are only present in appendages lacking fin rays and scales, which imply that paired fins of crownward tetrapodomorphs such as “elpistostegalians” or tetrapods can carry either digits or lepidotrichia, but not both at the same time.

The median fins pattern of early tetrapods consist exclusively of a long, continuous, and well developed diphycercal caudal fin showing lepidotrichia in both dorsal and ventral lobes. As in "elpistostegalians" the dorsal lobe extends more anteriorly than the ventral one. Anal and dorsal fins are absent. Lepidotrichia articulate with a series of caudal fin radials (supraneurals for the dorsal lobe and suprahaemals for the ventral one), which in turn articulate with the neural and haemal spines respectively. This "fish-like" tail is lost in post Devonian tetrapods where the fin fold supported by endosqueletal radials and dermal lepidotrichia is replaced by an epidermal fin fold without osseous dermal components, as that of extant aquatic salamanders. We will restrict our description of the structure of the tetrapod tail to the two best known Devonian tetrapods with relatively well preserved postcranial and caudal skeleton with dermal fin rays: *Ichthyostega* and *Acanthostega* from the Late Devonian (Famennian) of East Greenland (Säve-Söderbergh, 1932; Jarvik, 1952). *Acanthostega* is considered as the sister group of *Ichthyostega, Tulerpeton* and all the more derived post Devonian tetrapods.

Lepidotrichia are known in the caudal fin of the Devonian tetrapods *Acanthostega gunnari* (Coates, 1996) and *Ichthyostega stensioei* (Jarvik, 1952, 1959, 1996). They were also very likely present in *Tulerpeton curtum* (Lebedev & Coates, 1995) for which the caudal skeleton is unfortunately not preserved, and other uncertainly assigned and incompletely known Devonian "tetrapods" (see above).

The lepidotrichia of *Ichthyostega* are short, stout bony rods that are unsegmented and unbranched throughout the ray. They are round in cross section, probably along the entire length of the ray, and generally of about the same length as the radials (Jarvik, 1952). The tapering proximal portion overlaps extensively the radials as in "osteolepiforms" and holoptychiid porolepiforms. The overlapped portion comprises more than two thirds of the total length of the ray. In *Ichthyostega* the lepidotrichia of the caudal fin are supported by the

radials and most posteriorly by a long horizontal radial bone [the so-called "urostyle" of Jarvik (1952)]. They greatly outnumber the radials, each radial carrying up to six lepidotrichia. The lepidotrichia extend more anteriorly in the dorsal lobe of the caudal fin than in the ventral one. On the dorsal lobe lepidotrichia are well developed and range from the posterior tip of the tail to a point little behind the postsacral ribs, whereas in the ventral lobe the lepidotrichia are extremely short and occupy only the most posterior region. The anterior radials of this ventral lobe do not seem to carry lepidotrichia (Jarvik, 1952).

In *Acanthostega* the morphology and arrangement of the lepidotrichia resemble those of *Ichthyostega,* although they encompass a greater part of the tail, and are relatively longer on both lobes, the longest of them being positioned at the extreme posterior end of the tail (Coates, 1996). As in *Ichthyostega*, they are unsegmented and unbranched for their entire length. The lepidotrichia of *Acanthostega* are more numerous than those of *Ichthyostega* and each radial can carry up to eight lepidotrichia (Coates, 1996). Preservation of the caudal fin does not allow measuring the degree of overlap between the radials and the lepidotrichia but according to Coates (1996) reconstruction the overlapped region would comprise about one fifth of the ray total length. As in *Ichthyostega* the dorsal lobe of the caudal fin extends more anteriorly than the ventral one. However the gap between them is not as large as in *Ichthyostega*. All the radials carry lepidotrichia, even those of the ventral lobe, as opposed to *Ichthyostega*.

Relying on a subtle anterior subdivision of the caudal fin of *Ichthyostega*, Jarvik (1959) stated that the long and continuous tail of tetrapods probably arose by the fusion of the caudal fin with the equivalent of the second dorsal fin of "osteolepiforms", a similar condition to the one proposed for the evolution of the long caudal fin of dipnoans (see above). However, *Acanthostega* shows no sign of subdivision whatsoever in its long and leaf-like shaped caudal fin (Coates, 1996), nor do "elpistostegalians" like *Panderichthys* (Vorobyeva & Schultze,

1991). Jarvik (1952) also considered that the lepidotrichia of *Ichthyostega* correspond to the unsegmented proximal portion of the lepidotrichia of other tetrapodomorph sarcopterygians (e.g., "osteolepiforms" and rhizodontids). Johanson et al. (2002) proposed that in tetrapods those long basal segments were not "true" lepidotrichia formed within the apical fin-fold. However, histological data confirm that the unsegmented lepidotrichia of Devonian tetrapods are formed by the same type of cellular bone as that of true lepidotrichia (Goodrich, 1904; Jarvik, 1952; Zylberberg et al., 2010). In that sense it is more parsimonious to consider that the unsegmented and unbranched lepidotrichia of Devonian tetrapods would have lost the capacity to joint and bifurcate in their distal portion and should not need to be considered as different structures with a different developmental origin from that of "common" lepidotrichia (Johanson et al., 2002).

"Fish-like" tails of Devonian tetrapods are not exclusively characterized by the presence of dermal fin rays, but by the combination of radials associated with these rays. Lepidotrichia and associated radials have not been recorded in any post Devonian tetrapod, and have generally been assumed to be absent in these derived forms. Based on paleontological data it is then plausible to assume a developmental relationship between radials and lepidotrichia in early tetrapods implying that the disappearance of one of these structures would lead to the disappearance of the other. Recent findings have shown that caudal fin radials (supraneural bones) were retained in certain Carboniferous groups such as embolomeres (Clack, 2011) and therefore a caudal fin supported by endosqueletal elements (radials) and possibly lepidotrichia, would not be totally unexpected in aquatic Carboniferous tetrapods. Developmental evidence of the relationship between radials and lepidotrichia will be discussed later.

To sum up, Devonian tetrapods retain lepidotrichia associated with the radials in their caudal fins; however these fin rays are unsegmented, unbranched and differently sized in the

two best known Devonian taxa: *Acanthostega* and *Ichthyostega*. The absence of lepidotrichia in the anterior part of the ventral lobe of the caudal fin and the modifications of the radials in this tail region in *Ichthyostega,* and more subtly in *Acanthostega*, show that even if the the tail certainly was used mainly for aquatic locomotion, it rested or partially dragged on the ground when the animal was on land or in shallow waters. Interestingly polydactylous limbs are found in Devonian tetrapods retaining "fish-like" tails. The stabilisation of pentadactylous limbs in Carboniferous tetrapods seems to be correlated with the disappearance of lepidotrichia in the caudal fin.

## ACTINOPTERYGII

(Manuel MARÍ-BEFFA)

Actinopterygii comprise all ray-finned fishes. Actinopterygii are highly diverse with two subclasses, 42 orders, 431 families, 4075 genera and 23681 species (Nelson, 1994) and are also world-wide distributed in any water ecological niche. Whereas subclass Chondrostei may be paraphyletic, subclass Neopterygii is thought to be a monophyletic group. The definition of this class involves scales, pectoral radials (elements of endochondral bones), interopercular and branchiostegal rays or nostril position in the head, but the most outstanding character for taxonomy of this class is the fin. Actinopterygii originate during Late Silurian and the early Devonian (Arratia and Cloutier, 1993).

Actinopterygian fishes show paired and median fins. Paired fins are pectoral and pelvic fins, whereas median fins are dorsal, anal and caudal fin. Each fin is composed of a basal endochondral skeleton and a distal dermal skeleton. The dermal skeleton is composed of branched, segmented rays and spines inmersed in a continuous interray or interspine membrane which connects each skeletal element. Whereas the spines are solid, the soft-rays are composed of two contralateral bracket-like hemi-rays. Number of branching/unbranching rays or spines, position and length of fins are species-specific characters very useful in taxonomy of this group of tetrapods (see Nelson, 1994). Fins are also vascularized and innervated in a species-specific manner. As a general pattern, an irrigating capillary blood vessel usually occurs in the centre of the ray and two draining capillaries are commonly observed in the ray-interrays boundary. These capillaries may also be interspersed through interrays and other ray positions in a continuous plexus in model species (Bayliss et al., 2006). Two contralateral symmetrical nerves are observed underneath both hemirays (see Becerra et al., 1983). Pigment cells are extremely variable in position and types, being

common iridocytes and melanocytes (see Hawkes, 1974). Marginal rays in the fins may gradually vary in length or abruptly be reduced in size, as the procurrent rays. In the latter fins with branching rays, the anteriormost long ray/rays in all fins and the posteriormost long ray/rays in caudal fin are not branched. Posteriormost rays in the rest of fins may be branched and show a small posterior interray (see Nelson, 1994).

This general pattern is observed in actinopterygian fishes of all 431 living families involving most actinopterygian species (Nelson, 1994). However, variations in other features may be observed in an important number of taxa. Perciformes (Suborder Percoidei) fishes show two dorsal fins, the first one with spines and the second one with rays (Nelson, 1994). Median fins may also be fussed in species from many families, i.e. Cynoglossidae (Chapleau, 1988), Scytalinidae (Nelson, 1994), Zoarcidae (Nelson, 1984), Cepolidae (Smith-Vaniz in Smith and Heemstra, 1986), Notograptidae (Tyler and Smith, 1970), Muraenolepididae (Fahay and Markle, 1984), Pseudochromidae (Godkin and Winterbottom, 1985), Macruronidae (Howes, 1991b), Aphyonidae (Cohen and Nielsen, 1978), Ophidiidae (Nelson, 1994), Plotosidae (Gomon and Taylor, 1982) families and Anguilliformes order (Böhlke, 1989). All fins may be absent in specific families or genera. As an example, dorsal fins are absent in Gymnotiformes order (Mago-Leccia, 1978), anal fins absent in Gymnarchidae (Nelson, 1994), Trachipteridae (Palmer, 1961), Regalecidae (Nelson, 1994) families, caudal fins absent in Gymnarchidae (Nelson, 1994) family, pectoral fins absent in Symbranchidae (Rosen and Greenwood, 1976) or Sygnatidae (Dawson, 1982a) families and pelvic fins absent in Anguilliformes (Böhlke, 1989), Gymnotiformes (Mago-Leccia, 1978) order, many species in Ophidiiformes (Cohen and Nielsen, 1978), Gadiformes (Cohen, 1989) order and Tetraodontidae (Nelson, 1994), Gymnarchidae (Nelson, 1994) or Zoarcidae (Nelson, 1984) families. In specific orders or families, such as Perciformes (Nelson, 1994) order or

Syngnathidae (Dawson, 1982a) family, may show absence of several fins, dorsal, anal or pectoral, Symbranchidae (paired fins, Rosen and Greenwood, 1976), Trichiuridae (pelvic and caudal fins absent, Parin and Bekker, 1972) families. In all fins, spines may be differentiated. The best example is the anterior dorsal fin of Perciformes which only shows spines (Nelson, 1994). In other instances, true spines are normally differentiated at the anteriormost margin of the fin. Examples are observed in Perciformes (Nelson, 1994) or Acanthomorphs (dorsal, anal and pelvic fins, Rosen, 1973a). However, spine-like rays may also be differentiated in Gadiformes, Macrouridae or Merlucciidae (dorsal fin, Marshall and Iwamoto, 1973 or Cohen et al., 1990) families, Batrachoidiformes or Ophidiiformes (Pelvic fins, Patterson and Rosen, 1989 or Cohen and Nielsen, 1978), Lophiiformes (dorsal and pelvic fins, Pietsch, 1984a), Siluriformes (dorsal and pectoral fins, Howes, 1983a; Schaefer, 1990) or Percopsiformes, Albuliformes (Notacanthidae, dorsal and anal fins, Rosen, 1985 or McDowell, 1973) orders. Rayless fins have been described in *Leucobrotula adipata*, fam. Parabrotulidae, *Benthocometes robustus*, fam. Ophidiidae, *Nettastoma melanurum*, fam. Nettastomatidae, *Mola mola*, fam. Molidae, *Hymenocephalus italicus*, fam. Macrouridae, *Liparis fabricii*, fam. Liparididae, *Angilla anguilla*, fam. Anguilliidae, *Conger conger*, fam. Congridae, *Govania wikdenowi*, fam. Gobiesocidae, *Lepadogaster lepadogaster lepadogaster*, fam. Gobiesocidae, *Lepadogaster candollei*, fam. Gobiesocidae, species. Finally, fins without skeleton (i.e. adipose fins) can be observed in many families from Characiformes (Géry, 1977), Siluriformes (Howes, 1983a; Schaefer, 1990), Salmoniformes (Fink and Weitzman, 1982) orders.

Soft-ray morphology may also show important variations in this clade. Rays may be normally branched (i.e. Balitoridae family, Sawada, 1982) or only distally (i.e. *Astronestes cyclophotus*, fam. Astronesthidae, *Sardina pilchardus*, fam. Clupeidae, *Sprattus sprattus*, fam.

Clupeidae, *Coryphaena hippurus*, fam. Coryphaenidae, or *Chaulodis sloani*, fam. Chaulodiothidae, species). Fin rays are normally segmented in most members of almost all fish families, or only distally. But rays may also be unbranched or unsegmented or both in many different species scattered among all actinopterygian families. Examples of fins with unbranched rays are Psilorhynchinae (Rainboth, 1983) subfamily, *Agonus cataphractus* (Agonidae), *Anarhichas denticulatus* (Anarhichadidae), *Clinitrachus argentatus* (Clinidae), *Histrio histrio* (Antennariidae), *Bathylagus euryops* (Bathylagidae) or *Cepola rubescens* (Cepolidae) species. Examples of unsegmented rays are found in Congridae (see Böhlke, 1989) or Pleuronectidae (Li, 1981). Finally, examples of unbranched and unsegmented rays are found in ** species. An interesting feature is the partial disappearance of segments and branches in a huge variety of actinopterygian species. This is related to the anteroposterior gradient pattern of branching rays observed in many dorsal and anal fins (branching in anterior rays are distal whereas in posterior rays, proximal, i.e. *Gobius auratus*). When branching disappears resemble a "distalization" phenotype in which anterior branches disappear and gradually appear to more proximal positions in posterior rays (i.e. *Dicologlossa azevia*, *Dicologlossa cuneata*, *Lipophrys pavo*, *Lipophrys trigloides*, *Callionymus risso*, *Microchirus ocelatus*, *Microhirus hispidus*, *Lepadogaster cuitus*, *Lepadogaster candollei*, *Lepadogaster conchii*, *Pegusa lascaris*, *Pomatochistus knerii*, *Solea senegalensis*, *Acanthocottus lillyeborgi*, *Xenodermichthys copei*, fam. Aleprocephalidae, *Pterycombus brana*, fam. Bramidae, *Callionymus lyra*, fam. Callionymidae, *Dactylopterus volitans*, fam. Dactylopteridae, or *Merluccius merluccius*, fam. Merlucciidae). Even in the same family, species can be found to show segmented, completely unsegmented and partially unsegmented rays (Phycidae family, Markle, 1989). In these cases, as in the rest, a phenotypic series of morphologies can be observed. The loss of segmentation is initially observed in proximal positions gradually extending to more distal positions in other species until the complete

unsegmented phenotype is found. A similar trend is observed when ray branching is considered. In Gobiidae family, *Didogobius* or *Neogobius* genera, Triglidae family, *Lepidotrigla* genus, Cyclopteridae family, *Eumicrotremus* genus, Callionymidae, Platycephalidae or Scorpaenidae families, species with this phenotype can be found (i.e. proximal branches of rays are found in *Eumicrotremus derjugini* which gradually distalize in other species, such as *Eumicrotremus terraenovae*, to finally disappear at distalmost positions in *Eumicrotremus spinosus* species). Another example is *Neogobius melanostomus* (proximal), *Ponticola eurycephalus* (distal) and *Neogobius fluviatilis* (unbranched rays). These phenotypes are shown without any other special modification of ray isolation, enlargement or specific morphological modifications, such as loss of segmentation, as those shown associated to fertilization functions, e.g. the gonopodium in Poecillidae (see Zauner et al., 2003) or Anablepidae (Parenti, 1981) families, the priapum in Phallostethidae family (Parenti, 1986) or the contact and intromittent organs of *Horaichthys setnai* (Hubbs, 1941; Parenti, 2008). However, nongradiental unbranching patterns can also be found as local unbranching rays neighbour to normal branching rays in Esocidae (Crossman, 1978) or Umbridae (Nelson, 1994) families.

This diversification of morphologies is often associated with a variety of functional co-options. Among these co-options, flying (Exocoetidae family, Collette et al., 1984), sexual attraction (Poeciliidae family, Basolo, 1990), chemical defence (Batrachoididae family, Thalassophryninae subfamily, Halstead, 1967-70), adherence to substratum (Gobiesocidae family, Briggs, 1955), fishing (Lophiiformes order, Pietsch, 1984a), "walking" (*Dactylopterus volitans* species, Nelson, 1994), are some examples in which rays or ray transformation may fulfil new functions.

**DISCUSSION** (Jorge MONDÉJAR-FERNÁNDEZ)

Fin and fin rays development have been well studied by developmental biologists since the end of the XIXº century (e.g., von Baer, 1853; Huxley, 1859) and a large amount of bibliographical references deal with the morphological and molecular features of fin ray development and regeneration (see a review by Marí-Beffa & Murciano, 2010 and references therein). Indeed, fin rays are a good tool in the understanding of vertebrate ontogenetic development (Cloutier, 2010) and allow comprehending more deeply the connections between gene expression (during normal development, regeneration, and mutagenesis) and morphological and structural variation of anatomical traits.

Fin ray development has been thoroughly studied in osteichthyans through the zebrafish *Danio rerio* (Marí-Beffa & Murciano, 2010), the most universal model organism in the study of early vertebrate anatomy and development (Metscher & Ahlberg 1999). Other studies on fin ray anatomy and development have been performed mostly in extant actinopterygians such as *Salmo* (Géraudie & Landis, 1982), *Oncorhynchus* (Charest & Cloutier, 2009), *Medaka* (Iwamatsu, 2004), *Tilapia* (Becerra et al., 1983), *Amia* (Grande & Bemis, 1998) *Polyodon* (Bemis & Grande, 2000; Davis et al., 2004b), and *Acipenser* (Davis et al., 2004b), but also in sarcopterygians such as the dipnoans *Neoceratodus* (Goodrich, 1906; Hodgkinson et al., 2008), *Protopterus* (Géraudie & Meunier, 1984), and *Lepidosiren* (Arratia et al., 2001), and the coelacanth *Latimeria* (Géraudie & Meunier, 1980; Castanet et al., 1975).

The biological development of any organic structure is driven by genetic determinism and environmental influences, both during embryological and adult development (i.e., ontogeny). Understanding the relationships between development and environment will shed more light in our understanding of the evolutionary processes ocurred during the evolutionary history of osteichthyans, and more particularly in the evolution of fins and fin rays. Therefore,

it is extremely usefull to describe the general developmental pattern for the fins of bony fishes, in order to highlight a common pattern from which particular morphologies could derive. By doing so, we will be able to identify which part, or stages, of the developmental pathway are more likely to have been modified or afected during the evolution of osteichthyan groups, and to what extent such modifications could have been correlated with changes in the mode of life. The key example of this approach is that of the origin of tetrapods from tetrapodomorph sarcopterygians during the Devonian (see above).

In the following sections we will describe and review: 1) the common morphogenetic developmental process of fin (paired and median) formation in the Osteichthyes synthesized from data from both actinopterygians and sarcoptergians; 2) the stablishment of a referencial frame of study based on axis polarity and patterning of the fin rays; 3) the main phylogentic trends in the evolution of fin ray morphology and structure in osteichthyans and their relationships with environmental and lifestyle changes; and 4) a new and complete developmental, morphofucntional, and evolutionary scenario for the evolution of fins and fin rays during the 'fish-tetrapod transition'.

## 1. Developmental processes during fin morphogenesis

Paired and median fins in vertebrates have different embryological origins but share similar developmental mechanisms (Freitas et al., 2006). Both fin types are generally composed of a basal endoskeleton and a distal dermoskeleton, but beside this structural uniform pattern, there are major differences in the number and arrangement of the endoskeletal bones between paired and median fins. Median fins arise predominantly from somitic (paraxial) mesoderm, whereas paired appendages develop from lateral plate mesoderm (François, 1958; Freitas et al., 2006). However, the genetic pathways involved in

the differentiation of both paired and median fins are extremely similar. It has been shown that the molecular mechanisms for fin development originated in somitic mesoderm of early vertebrates, and that the origin of paired fins was associated with the re-deployment of these mechanisms to lateral plate mesoderm (Freitas et al., 2006). Such developmental mechanisms are probably conserved since the origin of gnathostomes and might reflect the ancestral state of vertebrate appendage organizers (e.g., Sordino et al., 1995; Freitas et al., 2006; Dahn et al., 2007; Hadzhiev et al., 2007).

***Fin development***

**Paired fins –** The paired fins of the zebrafish, as representatives of the general osteicthyan condition to a certain extent (Metscher & Ahlberg, 1999), have been thouroughly studied and the succesive developmental stages and genetic pathways directing development are relatively well known (Marí-Beffa & Murciano, 2010).

The initiation of paired fin development involves the transfer of positional information from the somitic mesoderm to the intermediate mesoderm (IM), then to the lateral plate mesoderm (LPM), and finally from there to the ectoderm (Fischer et al., 2003). Genetic evidence indicates that diffusing retinoic acid (RA) from the somites is required for signalling activation in the IM. Wnt2b (pectoral fin) and Wnt8c (pelvic fin) induce the T-box transcription factors, which are among the earliest known genes expressed in the paired fin mesenchyme; Tbx5 is expressed in the pectoral fin whereas Tbx4 is expressed in the pelvic fins (Mercader, 2007), exactly as in tetrapod fore and hindlimbs (Gibson-Brown et al., 1996). This results in the formation of a small bud by localized mesenchymal cell proliferation under the ectoderm.

Subsequently, an apical ectodermal ridge (AER) is induced by mesenchymal signals. The AER consists of a thickening of the ectoderm layer located at the distal margin of the fin bud that runs along its anteroposterior axis. Mesenchymal fibroblast growth factor (Fgf) signalling from the underlying mesenchyme induces Fgf signalling from the AER and triggers the initiation of proximodistal (PD) outgrowth of the bud. The AER is thus an essential organizer for the outgrowth and proximodistal patterning in fin bud development.

The anteroposterior (AP) patterning of the fin bud is stablished by a second organizer known as the zone of polarizing activity (ZPA), consisting of a group of cells located in the distal posterior mesenchyme. The ZPA diffuses sonic hedgehog (Shh), which becomes part of a Shh–Fgf feedback loop between the ZPA and the AER that coordinates cell proliferation along the antero-posterior axis. Although the activity of Shh here was at first thought to be a derived osteichthyan feature it is now known to be present also in chondrichthyans, performing much the same role (Dahn et al., 2007).

Next, the AER is modified into the apical fold (AF) as the basal ectodermal stratum folds into a double-layered epithelium. In tetrapod, this folding does not occur, and constitues one of the main developmental differences between fishes and land vertebrates. Neverthless, it has been shown that the AF also expresses similar molecular markers to the tetrapod AER, particularly Fgfs, suggesting that the AR in fishes fulfills the same functions as the AER in tetrapods (Mercader, 2007). In teleosts and basal actinopterygians the development of the fin fold is coincident with the first stages of chondrogenesis of the endoskeletal disc (Grandel and Schulte-Meker, 1998; Davis et al., 2004b). The proximal mesenchyme condenses to give rise to the cartilage-forming endoskeletal bones, whereas the AF will house the larval fin dermoskeleton. First, collagenous actinotrichia develop within the AF, strengthening it. Then, mesenchymal cells migrate into the AF and differentiate into scleroblast that will build the osseous lepidotrichia using the actinotrichia as a scaffold. Thus, it appears that the

actinotrichia play a role in organizing mesenchymal invasion of the AF, perhaps through a mechanism of contact guidance (Wood and Thorogood, 1984).

It is considered that both paired fins develop in a general similar way; however there are some major differences between them. The pectoral fin is always the first paired fin to form. In actinopterygians, the pectoral fin develops in two phases: a "larval" phase in which a chondrogenic condensation supported with actnotrichia forms a large basal endosketal disc, and an "adult" phase during which the fin radials develop from division, reconstruction, and local decomposition of the cartilaginous endoskeletal disc, a chondrogenic plate of mesenchymal cells; lepidotrichia form and ossify during the "adult" phase before the radials (Grandel & Schulte-Meker, 1999; Davis et al., 2004b). The loss of the propterygium and mesopterygium in sarcopterygians signifies the origin of the stylopod, and has been proposed to be developmentally achieved through the loss of the endoskeletal disc still present in actinopterygians (Davis et al. 2004b).

Little is known about the development of the pelvic fins, which develop much later that the pectoral fins. One notable difference between pectoral and pelvic fins is that the latter do not show a "larval" phase as in the pectoral fins, but rather develop directly into the adult form whithout forming an analogous endoskeletal disc (Grandel & Schulte-Meker, 1999).

**Median fins –** The median fins include the dorsal(s), anal, and caudal fins. In zebrafish the caudal fin develops first, as in the vast majority of fishes, followed by the anal and finally the dorsal fin(s). Of the dorsal and anal fins, the more posterior fin develops before the more anterior fin.

Development of median fins is similar in certain aspects with that of paired fins, but differs in others. Median fins form following a continuous dorsal and ventral fin fold present since the earliest ontogentic stages. As in paired fins, an AER forms transiently and then is

transformed into the so-called median fin fold (MFF) (Abe et al., 2007). In the beginning of median fin formation, the two epithelial layers start to separate from the body wall and from each other; the space between the fin fold and the dorsal and ventral somites is invaded by mesenchymal cells that proliferate forming a fin bud, similar to that of paired fins. Actinotrichia begin to form whithin the distal fold and the proximal mesenchyme condenses into the cartilage-forming endoskeletal bones. As in paired fin, mesenchymal cells, *probably of neural crest origin*, penetrate the distal fin fold and differentiate into scleroblast that will build the osseous lepidotrichia using the actinotrichia as a scaffold. The source of these mesenchymal cells is still a matter of speculation. According to Géraudie and François (1973) and Schaeffer (1977), they derive, in paired fins, from thickenings of the somatic layers of the lateral plate mesoderm and undergo interactions with the overlying epithelium. In contrast, trunk neural crest may induce the median fin fold and provide the mesenchyme occupying the center of the fold (Schaeffer 1977). Smith et al. (1994) provided the first, and so far only, experimental evidence that cells of neural crest origin populate the caudal fin in the zebrafish and thus potentially contribute to lepidotrichial formation.

***Differences between fin and limb formation***

Paired fish fins and tetrapod limbs are homologous organs, they share a common evolutionary ancestry and a common developmental origin, i.e., both fins and limbs develop through similar developmental processes and genetic networks but show nevertheless remarkable morphological differences due to their separate evolutionary history (Tamura et al., 2001). However, fins and limbs do not differ exclusively on their morphology, there are also important and/or subtile differences in the genetic pathways involved in their formation. Such differences in the genetic network and morphogenetic development between fishes and

tetrapods probably evolved to solve different problems arising from different morphological constraints (Mercader, 2007). However, it has been shown that the role of key molecules involved in limb/fin formation (e.g., RA, Tbx, Shh, Fgs, etc.) is conserved independently of their evolutionary history. The lack of role conservation of other molecules could be due to their modulatory expression rather than essential functions. Alterations in gene regulatory networks are likely to be the basis for the morphological diversification of appendages (fins or limbs) in different groups of vertebrates.

The tetrapod limb can be clearly divided into three domains: stylopod, zeugopod, and autopod. The stylopod consists of a single long bone (humerus/femur) articulating with a girdle (pectoral/pelvic, respectively). The zeugopod is composed of two long bones (radius/ulna in forelimb and tibia/fibula in the hindlimb). The autopod includes many bone elements that can be subdivided into carpal/tarsal bones, metacarpal/metatarsal bones, and phalanges; the number of bones varying among taxa.

The paired fins of osteichthyan fishes do not show these three domains (although the stylopod characterises sarcopterygian, and it is considered that the zeugopod appeared with tetrapodomorphs). However, the fins of actinopterygians can also be divided into three portions: proximal radials, distal radials, and fin rays (Grandel & Schulte-Merker, 1998; Davis et al. 2004b). The proximal radials (four or more in number) are columnar bones at the proximal-most domain and are located distal to the pectoral/pelvic girdle. Distal to the proximal radials, there is a line of pea-like distal radials. These two layers of skeleton are formed as endoskeleton, like the limb skeleton, but they occupy only a small portion of the entire fin structure. The major component of the fin skeleton is the fin rays, located in the distal-most portion forming a fin web, both in actinopterygians and sarcopterygian fishes, however more reduced in the latter.

It is thus clear that fins and limbs must have different developmental mechanisms that generate their morphological characteristics. However, despite these differences both fins and limbs share basic mechanisms for the initiation and outgrowth of the appendage primordia. During subsequent limb and fin outgrowth, the bud mesenchyme becomes patterned along three main axes: anteroposterior (AP) regulated by Shh (Harfe et al. 2004; Zeller et al. 2009), dorsoventral (DV) regulated by Wnt7a and En1 (Loomis et al. 1998), and proximodistal (PD) regulated by apical ectodermal ridge (AER) signals such as Fgfs (Kengaku et al. 1998; Fernandez-Teran & Ros, 2008; Lu et al. 2008). During this process, different signalling centers supply limb/fin bud cells with the positional information they need in order to differentiate into the appropriate element according to their location within the limb or fin. Signaling along these three axes is coordinated and interdependent and has proven to be conservative in osteichthyans (Grandel et al. 2000; Neumann et al. 1999; Yonei-Tamura et al. 2008; Dahn et al. 2007).

A major difference between fish and tetrapod paired appendage buds is the different fates of the AER, which is a transient structure in zebrafish embryos that is later replaced by the apical fold (AF), whereas in tetrapods it is maintained throughout the early development until the formation of the autopod. As previously described, the AF of fishes will house the actinotrichia and then the lepidotrichia that will constitute the fin web. In tetrapods the lack of AF impedes the formation of dermal fin rays in the paired fins and somehow enhances the development and outgrowth of the endoskeleton. The now classical “clock model” proposed by Thorogood (1991) states that variation in the endoskeletal pattern between fishes and tetrapods is caused by variation of the timing of the AER–AF transition; a less-patterned endoskeleton is formed by short exposure to AER signals, and a limb-like pattern is formed by longer exposure to AER signals than that of the less-patterned skeleton. The assumption underlying Thorogood’s model is that development of the endoskeleton and the dermal

skeleton are separated temporally and spatially (Shubin and Davis 2004; Davis *et al*. 2004a). Therefore, since fin-ray formation replaces endoskeleton formation after the AER–AF transition, it is possible that AF formation could have an inhibitory factor for outgrowth, patterning, and distal addition of the endoskeleton along the PD axis in fin development. Although not explicitly stated, this model implies that endoskeletal and lepidotrichial are each given a portion of a fixed 'time budget' of overall bud development (Jeffery, 2001).

However, the morphology of certain fossil sarcopterygians (e.g., rhizodontids and "elpistostegalians") fins does not fit with this model, as they show an equally important contribution from both endoskeletal and lepidotrichial elements. Furthermore, the endoskeleton displays an extremely complex pattern of segmentation (Jeffery, 2001 ; Shubin et al., 2006). It seems that the evolution of an increased complexity of the endoskeleton does not depend on the lack of transformation of the AER into the AF (thus reducing or losing the lepidotrichia). Indeed, recent work on the basal actinopterygians, *Polyodon* and *Acipenser*, indicates that there is an overlap between endochondral and dermal skeletal development during fin morphogenesis (Davis *et al*. 2004a).

The loss of the fin-fold may be rather related to the modification of gene expression, and asymmetric growth in the progress zone, both of which are unique to tetrapods (Nelson et al., 1996; Sordino et al., 1995). Thus in these limb-like fins, the 'time budget' must have been more flexible than supposed, allowing extended development of both endoskeleton and lepidotrichia. Hogkinson et al. (2009) showed that the developmental pattern of the pectoral fin of *Neoceratodus* does not completely support Thorogood's model (1991) either, because a fin fold leading to the formation of the dermal skeleton occurs concurrently with an AER and that the patterning of the proximodistal endoskeleton in lungfish occurs in two phases, i.e. AER phase and post-AER phase, probably under different molecular controls.

Recently Yano and Tamura (2012) proposed that the developmental mechanisms for the limb endoskeletal pattern (the PD separation of HoxA expression and AP expansion of 5‘HoxD expression) are discontinued by AF formation (AER-to-AF transition). Skeletal variations in the zeugopod and autopod of limb-like fins could thus be due to an incomplete regulation of the PD patterning by HoxA and of the AP expansion by 5’HoxD. This incompleteness may also be caused by the later timing of AF formation. Accordingly, The loss of the AF coincides with the acquisition of the autopod provided by the complete functions of HoxA and 5’HoxD (Yano and Tamura, 2012).

## 2. Fin Ray Patterning

As previously described, both fins and limbs are patterned in a very similar way following three main axes of development : proximodistal (PD), anteroposterior (AP), and dorsoventral (DV) for paired fins, or contralateral (CL) for median fins. We have highlited the similarities and differences between limb and fin formation, the main one being the establishment of the AF in fishes that give rise to the fin web, whereas its lack in tetrapods enables the development of the distal autopod. It has also been widely illustrated that fin ray formation follows and is somewhat dependent on the formation of endoskeletal elements in the fins.

Here we propose that since normal fin and limb development, and therefore all the skeletal elements housed in the fins or limbs, can be described and studied along three developmental axes, fin ray development and patterning can also be parted in such three axes (Marí-Beffa and Murciano, 2010). Moreover, these three axes have been referred to be independtly regulated (Murciano et al., 2007; Marí-Beffa & Murciano, 2010) and yet are interdependent on the formation of the fin rays; their interrelationship accounts for all the morphological and development diversity of the fin rays in osteichthyans.

Herein we will separate the morphological and developmental evidences in fin ray formation along each of the three axes, proximodistal (PD), anteroposterior (AP), and contralateral (CL), and discuss and contrast the morphological observations with the known genetic pathways involved in fin ray formation.

### 1) Proximodistal axis

***Morphological patterning*** – Several morphological aspects of the fin ray (both actinotrichia and lepidotrichia) formation can be described under the reference of the PD axis. Such aspects are at the same time ontogenetic and evolutionary

Formation of the actinotrichia

Formation of the lepidotrichia (following the PD patterning of the fin radials)

Distalization of the actinotrichia

Segmentation of the lepidotrichia

Ossification of the lepidotrichia (following the PD patterning of the fin radials)

Fusion of proximal segments

Bifurcation of the lepidotrichia (PD component applied to only one lepidotrichium)

Loss of actinotrichia

Loss of bifurcation

Loss of segmentation

***Developmental patterning*** –

### 2) Anteroposterior axis

***Morphological patterning*** –

Increase in lepoditricium width (coupled with the CL axis)

Ray-interray width (pinnamere width)

Bifurcation of the lepidotrichia (AP component)

Absence of bifurcation of the lepidotrichia

***Developmental patterning*** –

### 3) Contralateral axis

***Morphological patterning*** –

Cosmine and odontogenic components present in the outer surface (epidermal-dermal interactions)

Lack of internal calcification in the camptotrichia

Increase in ray width (coupled with the AP axis)

Differences in hemilepidotrichial width (asymmetrical hemilepidotrichia)

***Developmental patterning*** –

## 3. Phylogenetic trends in fin ray evolution

### Fin rays and convergence

### Fin rays and heterochrony

### Fin rays among fins

### Fin rays modules

## 4. The 'fish-tetrapod transition'

- The unsegmented and unbranched lepidotrichia of the caudal fin as a heterochronic (paedomorphic) character in tetrapod evolution (already proposed by Long, 1989)
- The presence of caudal lepidotrichia could be due to the pattern of maintenance of primitive characters in the tail of fishes (characters related to locomotion, such as fin rays, would be more "difficult" to loose in the tail than in other regions of the body). A parallel condition can be found in the tail of *Eusthenopteron* which develops first than other fins due to locomotor needs (Cote et al., 2002), the same is true for all fishes.
- The unsegmented and unbranched fin rays would represent the last stage in the gradual loss of fins and fin rays in crown ward tetrapodomorphs (e.g., "elpistostegalians" *Panderichthys* and *Tiktaalik*) following a proximo-distal patterning.

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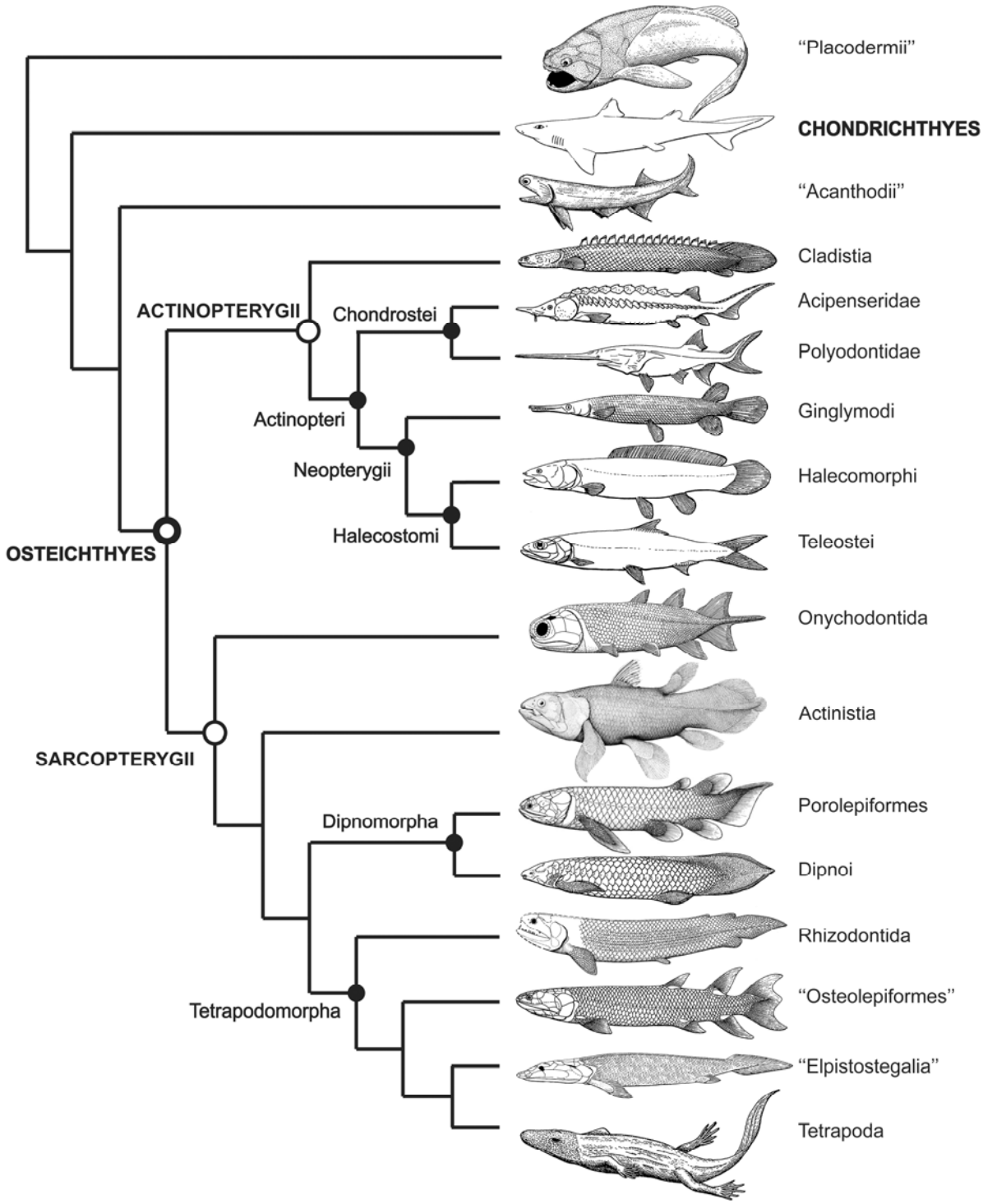
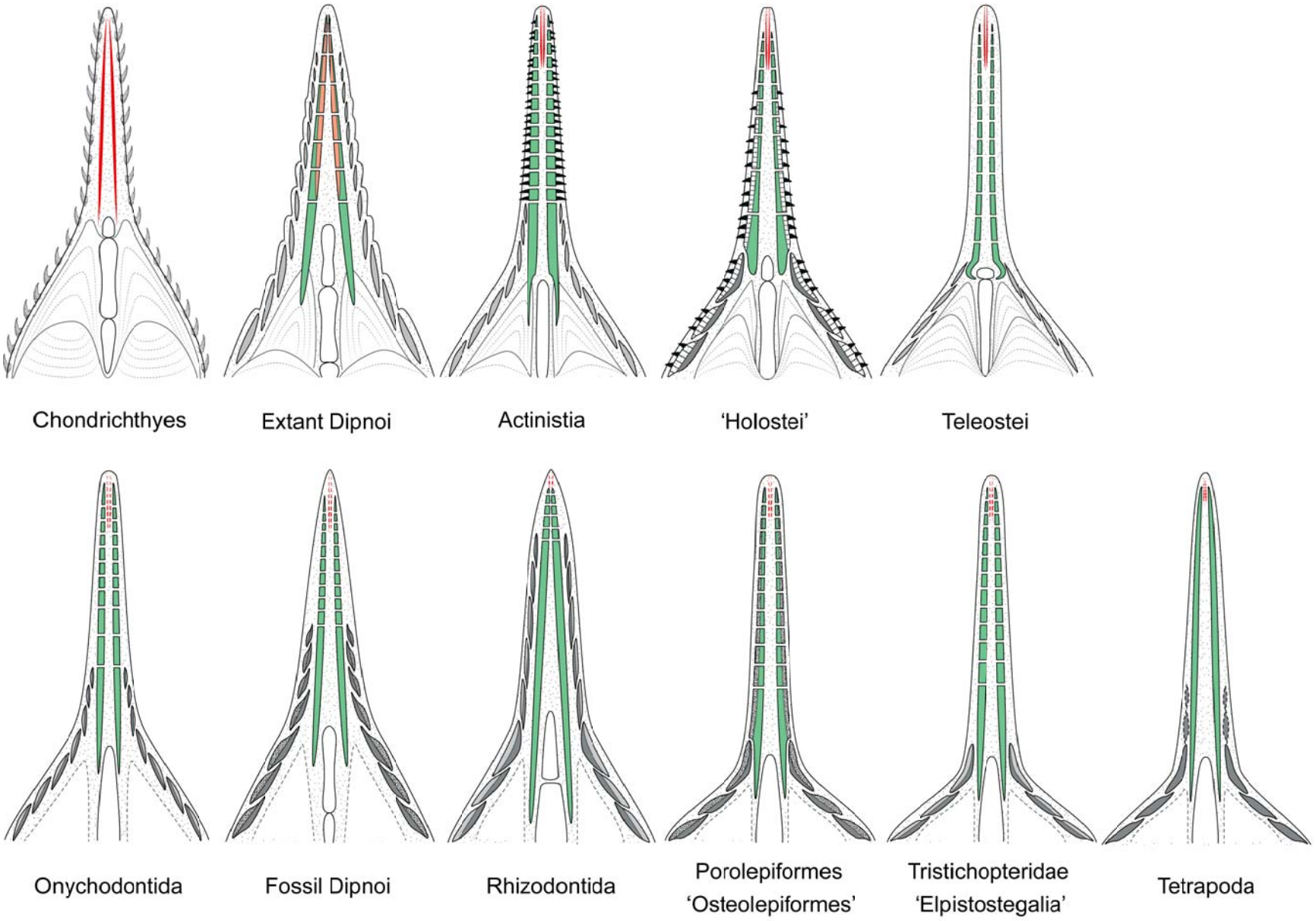



**FIGURE 1. Gnathostome phylogeny.** Consensual phylogeny with special reference to osteichthyan (actinopterygian and sarcopterygian) interrelationships. Drawings modified after Janvier, 1996.


Chondrichthyes
Extant Dipnoi
Actinistia
'Holostei'
Teleostei
Onychodontida
Fossil Dipnoi
Rhizodontida
Porolepiformes
'Osteolepiformes'
Tristichopteridae
'Elpistostegalia'
Tetrapoda

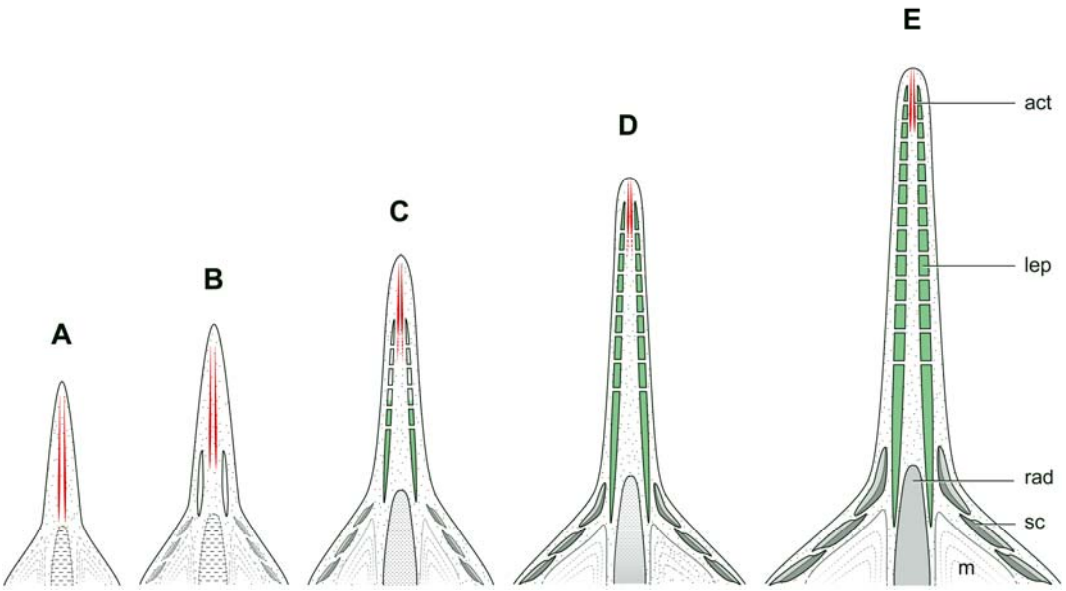



**FIGURE 2. Main ontogenetic stages during fin formation in osteichthyans. A.** Formation of the actinotrichia, differentiation of the radials; **B.** Early chondrogenesis of radials and initial differentiation of the lepidotrichia; **C.** Distal differentiation through distal addition of segments, proximal ossification of the lepidotrichia and proximal resorption of the actinotrichia; **D.** Distal ossification of the lepidotrichia, proximal ossification of the radials and proximal resorption of the actinotrichia; **E.** Bifurcation of the lepidotrichia (not seen) and complete ossification of the radials. Green colour shows ossification of the lepidotrichia. **Abbreviations: act**, actinotrichia; **lep**, lepidotrichia; **m**, muscles; **rad**, radial bone; **sc**, scale. Not to scale . Completed and modified after Géraudie & Landis, 1982.

**<< FIGURE 3. Diversity of dermal fin rays in fishes.** Schematic representation of the arrangement and structure of the dermal fin rays in the median fins of gnathostomes. **Chondrichthyes** (*Squalus*), **'Holostei'** (*Lepisosteus*), **Teleostei** (*Danio*), **Actinistia** (*Latimeria*), **Onychodontida** (*Onychodus*), **Fossil Dipnoi** (*Dipterus*), **Extant Dipnoi** (*Neoceratodus*), **Rhizodontida** (*Strepsodus*), **Porolepiformes** (cosmine-covered *Porolepis*), '**Osteolepiformes'** (cosmine-covered *Osteolepis*), **Tristichopteridae** (*Eusthenopteron*), '**Elpistostegalia'** (*Panderichthys*), **Tetrapoda** (*Acanthostega*). Lepidotrichia are represented in green and actinotrichia in red. Dotted actinotrichia correspond to their putative presence in fossil sarcopterygian taxa. Not to scale. Completed and modified after Goodrich, 1904; Jarvik, 1959.

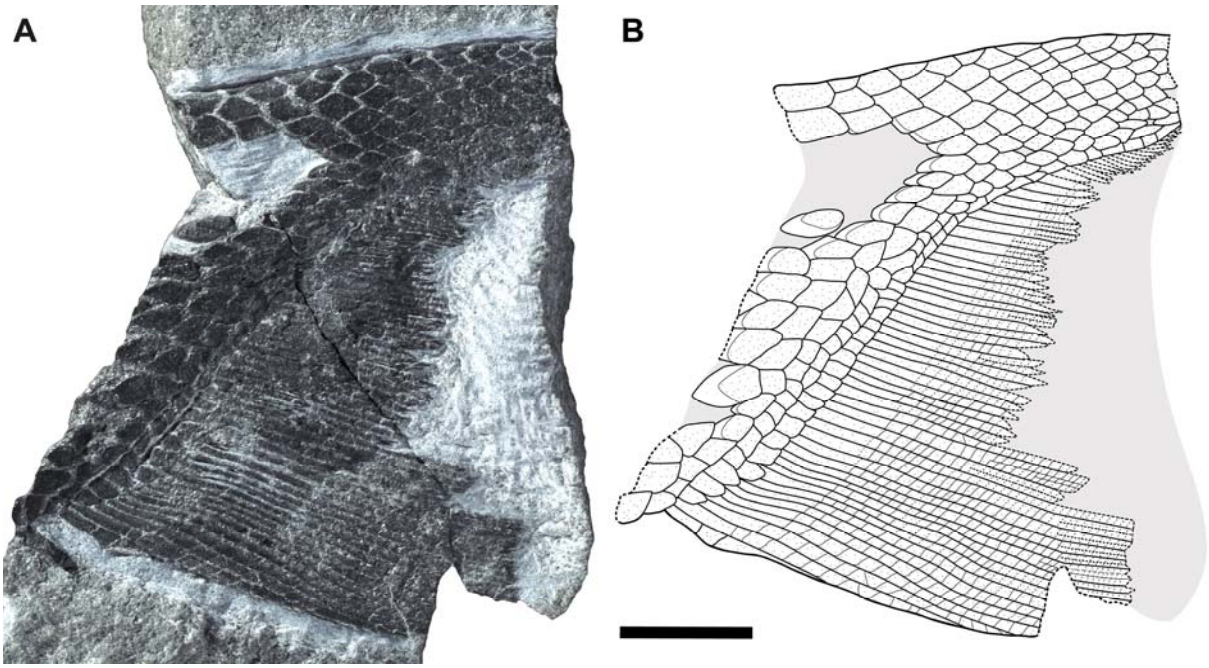



**FIGURE 4. Caudal fin of *Porolepis* sp., a porolepiform from the Early Devonian of Spitsbergen** (MNHN.f. SVD 4319 B). **A.** Photography of the specimen; **B.** Interpretative drawing. Dotted surfaces represent cosmine. Scale bar equals 1 cm.

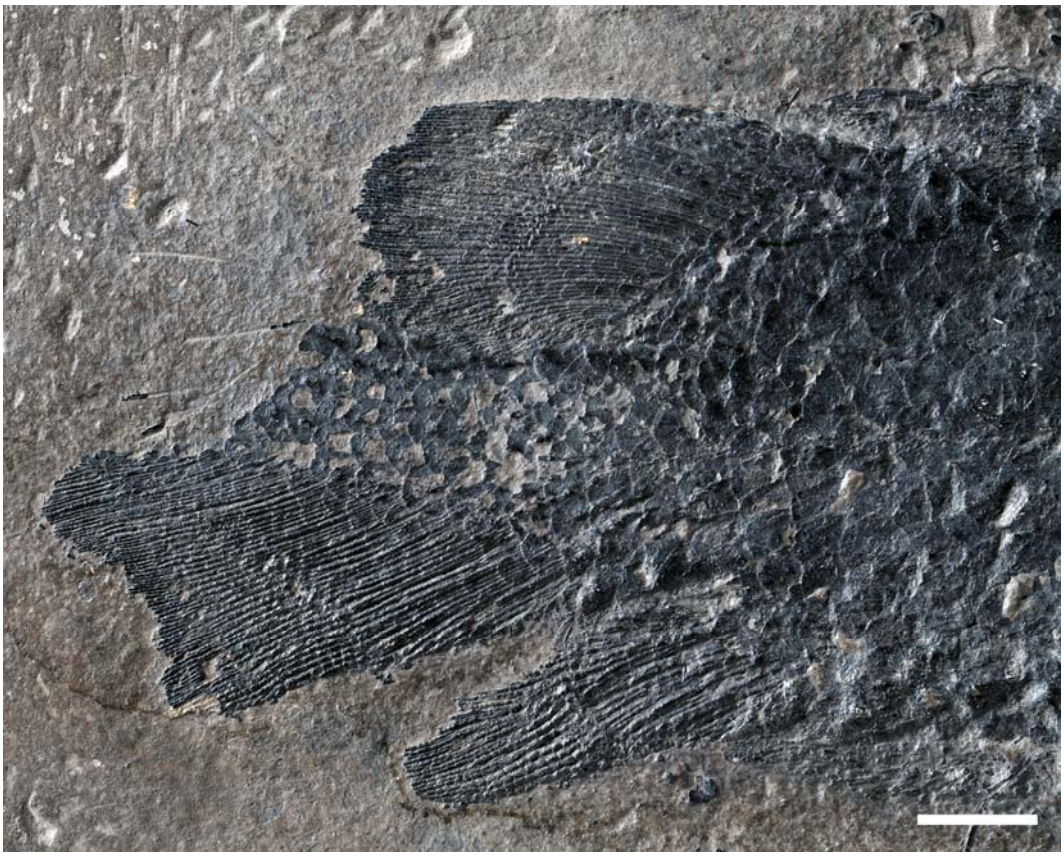


**FIGURE 5. Posterior half of the body of *Dipterus valenciennesi*, a dipnoan from the Middle Devonian of Scotland** (MNHN.f. GBP 386). Note the presence of rounded scale impressions over the unjointed proximal portion of the lepidotrichia of the second dorsal fin, anal fin, and hypochordal lobe of the caudal fin. Scales do not extend beyond the unsegmented portion of the lepidotrichia. Scale bar equals 1 cm.

**FIGURE 6. Second dorsal fin of *Scaumenacia curta*, a dipnoan from the Late Devonian of Québec, Canada** (MNHN.f. 1968.8.2 b). Arrow points anteriorly. Scale bar equals 1 cm.

**FIGURE 7. Posterior half of the body of *Scaumenacia curta*, a dipnoan from the Late Devonian of Québec, Canada** (MNHN.f. 1968.9). Scale bar equals 1 cm.

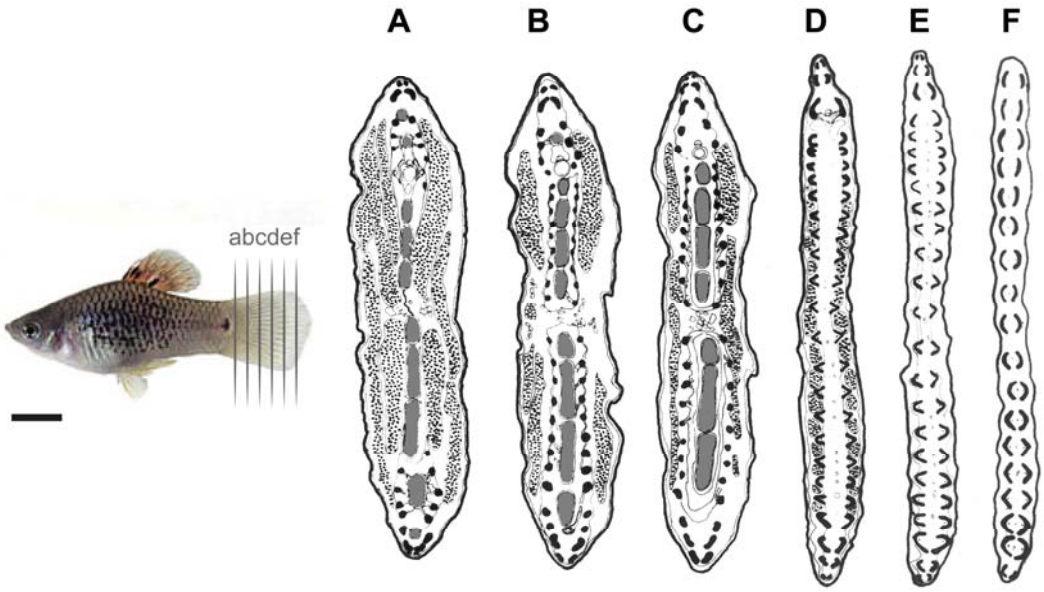
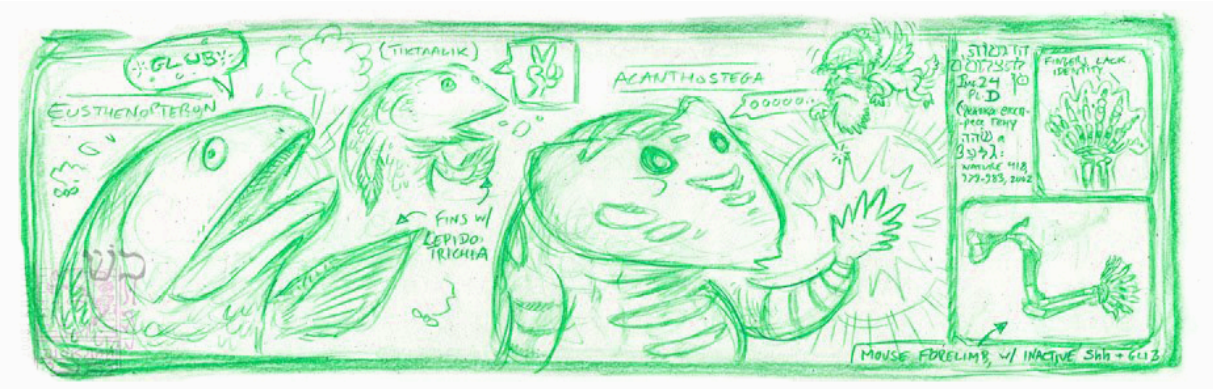



**FIGURE 8. Serial cross sections in the caudal fin of the female actinopterygian *Xiphophorus maculatus***. Note that in the proximal part of the fin, the hemilepidotrichia (in black) are rounded in cross sections and articulate with the fin radials (in grey) (A, B, C), whereas in more distal parts of the fin the hemilepidotrichia acquire the characteristic 'parenthesis shape' (D. E, F). Scale bar equals 1 cm; fin cross sections not to scale. Drawing courtesy of Manuel MARÍ-BEFFA.

# DISCUSSION


GLUB
EUSTHENOPTERON
(TIKTAALIK)
ACANTHOSTEGA
FINS W/ LEPIDO-TRICHIA
MOUSE FORELIMB, W/ INACTIVE Shh + 6113

# I. GENERAL INTEREST OF THE RESEARCH

Here I will present a synthesis of the main evolutionary issues encountered during this research. Several of these elements of discussion are obviously not supported by personal data (as opposite to the discussions of the Papers, sustained by their own new data) but are the result of thorough reflexions, personal observations, and readings throughout my thesis.

These discussions will deal with the evolutionary modifications of scales and fin rays in osteichthyans, with particular interest in Devonian sarcopterygians. Each section can work independently from each other and will consider either scales or fin rays. However certain sections will deal with common developmental aspects of both scales and lepidotrichia as a way of tackling the broad topic of the evolution of the dermal skeleton in vertebrates during the Palaeozoic.

# II. ON COSMINE

Cosmine is, without any doubt, one of the most puzzling structures in vertebrate evolutionary history. Cosmine has no extant representation among living forms and therefore the study of its *biology* (i.e., formation, resorption process, function, etc.) is one of the most intriguing and exciting questions in early vertebrate palaeontology (e.g., THOMSON, 1975). Former studies on cosmine have concentrated on single taxa, e.g., *Megalichthys* (WILLIAMSON, 1849; THOMSON, 1977; BORGEN, 1989), *Porolepis, Dipterus* and "osteolepidids" indet. (GROSS, 1956), dipnoans indet. (ØRVIG, 1969a), *Ectosteorhachis* (THOMSON, 1975), *Cladarosymblema* (FOX *et al.*, 1985), *Uranolophus* (CAMPBELL & BARWICK, 1992), *Gogonasus* (LONG *et al.*, 1997), and *Heimenia* (Paper I). The different

manifestations of cosmine in sarcopterygian were reviewed by MEINKE (1984) and hypotheses on cosmine formation and possible function were developed by ØRVIG (1969a), THOMSON (1975, 1977), BORGEN (1989, 1992), and BEMIS and NORTHCUTT (1992), among others.

Cosmine is found as a covering of the dermal bones and scales of Palaeozoic sarcopterygians. In the dermal bones, cosmine often occurs in large sheets that extend over a large number of otherwise separate dermal elements (e.g., bones of the skull roof and lower jaws), covering the sutures between them. Although cosmine is functionally a full constituent of the dermal skeleton, it is topographically and, to a great extent, also developmentally independent of the underlying constituents (THOMSON, 1975). As seen in the introduction, cosmine should not be considered a 'tissue', but a combination of tissues (enamel, dentine, and bone) and a structure (pore-canal system). Therefore, formation of the cosmine does not occur 'altogether', but rather represents an orchestrated development of enamel, dentine, and vascular bone that become intimately bound together. The dermal bone and odontogenic tissues (forming the pore-canal system) are essentially independent systems that have become juxtaposed. This perspective allows independent variation of the two systems during ontogeny and points toward a relationship between cosmine and other forms of odontogenic ornamentation of the dermal skeleton in early fishes (MEINKE, 1984).

Pore-canal systems similar to that of cosmine have been described in osteostracan "agnathans" (*Trematapsis*) (DENISON, 1951) and "acanthodians" (*Poracanthodes*) (GROSS, 1956). In osteostracans and "acanthodians", the pore-canal network is morphologically distinct to that of cosmine; the canals are enclosed in dermal bone and the vertical cavities open to the surface through pores in an enamel-like layer of dentine (schmelzartige oberste Dentinschicht, GROSS, 1956). The pore-canal systems

in osteostracans, “acanthodians”, and sarcopterygians represent parallel experiments in evolution, and are thus not considered homologous.

Explaining the formation and subsequent remodelling of cosmine during ontogeny is everything but simple. Cosmine, and other odontogenic tissues, are known to be capable of resorption during growth of the animal (FRANCILLON-VIEILLOT *et al.*, 1990) (Fig. II.1.1). WESTOLL (1936) first realized the necessity of resorption of cosmine to accommodate growth of the dermal skeleton. Subsequent studies on cosmine occurrence and growth (e.g., JARVIK, 1948, 1950; GROSS, 1956; ØRVIG, 1969a; THOMSON, 1975, 1977) have shown that each cosmine sheet represents a single depositional event. Cosmine is thus laid down by an essentially undivided cosmine field in the dermis and not as fused odontodes (*contra* the ‘lepidomorial theory’ of STENSIÖ and ØRVIG, see DONOGHUE, 2002), but this field may show traces of what could represent earlier ontogenetic stages when the pore-canal system was becoming organized under the form of isolated or superimposed dentine tubercles capped with enamel (i.e., odontodes).

The occurrence in adult cosmine of ‘ontogenetic traces’ is informative on the development and arrangement of cosmine during growth. SMITH (1977) suggested that early-formed odontodes made of dentine and enamel might represent the primitive condition in sarcopterygians. A single cosmine sheet was then acquired and further evolutionary changes might have proceeded in two directions: (1) preserving only the cosmine sheet, as in “osteolepidids” and “porolepidids”, or (2) retaining the early ontogenetic stage of denticles and no cosmine, characteristic of holoptychiids, derived dipnoans, onychodontids, and actinistians. The discovery of a cosmine-like structure in *Meemannia* (ZHU *et al.*, 2006) has refuted the primitive condition of isolated tubercles as proposed by SMITH (1977), and certainly implied by ØRVIG (1969a), but precised that the occurrence of a pore-canal system is tightly linked to the structure and arrangement of

the odontodes. The condition in *Meemannia* consists of three or four superimposed layers of odontodes separated by flask-shaped pore cavities interconnecting horizontal canals and pore openings (ZHU *et al.*, 2006, 2010). Each superimposed odontode carries a single layer of enamel, thus not corresponding properly to ganoine, but similar to it by the superimposed arrangement of layers. The unusual cosmine arrangement of *Meemannia* indicates that a pore-canal system is primitive for sarcopterygians, and that the establishment of a single sheet of cosmine and the ability to resorb previously deposited odontode layers evolved later in more crownward sarcopterygians. Histological comparative data on *Psarolepis* and *Styloichthys* were furnished by ZHU *et al.* (2010), but more thorough descriptions of these taxa are needed in order to illustrate the early stages of the evolution of cosmine.

The most challenging aspect of studying cosmine is the proposition of hypothesis concerning its function in living fishes. Since no extant sarcopterygian representatives possess cosmine, clues on its possible function had to be seek in the structure of the pore-canal system, resorption processes, and ontogenetic development in fossil forms. Propositions on the function of cosmine have been numerous, but the great majority of early studies assigned to the cosmine a role in the housing of sensory organs. Many researchers (e.g., MOY-THOMAS & MILES, 1971; THOMSON, 1975, 1977; NORTHCUTT & GANS, 1983; MEINKE, 1984; GANS, 1987) assumed that pore-canal systems, as present in "agnathans", "acanthodians", and sarcopterygians, primarily had a sensory (possibly electro-sensory) function. The pore-canal cavities would have housed a series of electroreceptory ampullary organs. However, certain studies on sarcopterygians have challenged this view.

BEMIS and NORTHCUTT (1992) showed that skin from the snout of *Neoceratodus* contains horizontal plexuses and vertical capillary loops that resemble in structure, size

and density to components of the cosmine from the dermal bones of the skull in Palaeozoic dipnoans such as *Dipterus* and *Chirodipterus.* Similarly, BORGEN (1992) proposed that the pore-canal system of the cosmine, at least in "osteolepidids" and porolepiforms, could have been primarily a vascular system and that the pore-canal cavities might have contained a vascular loop, or a sinusoid. Moreover, ZHU *et al.* (2010) showed that in *Meemannia*, the multiple layers of superimposed odontodes coexisting with one pore-canal network indicates that the pore-canal network does not have a one-to-one relationship to any single odontode layer.

This condition cast serious doubt on the belief that cosmine bears sensory and/or glandular function, which was inferred from the unique association of the pore-canal network with one single layer of odontodes and enamel in crownward sarcopterygians (rhipidistians, i.e., dipnomorphs and tetrapodomorphs). Moreover, MEINKE (1984) pointed out that electroreceptory ampullary organs do not communicate directly with each other. Thus, the system of horizontal canals connecting the vertical cavities is an argument against an electroreceptive function of the pore-canal cavities. Therefore, I agree that the primitive condition of *Meemannia* is more consistent with the function of cosmine as a vascular complex involved in the deposition and resorption of mineralized tissues, as proposed by BORGEN (1992) and BEMIS and NORTHCUTT (1992). 'True' cosmine, as present in rhipidistians (*sensu* Sire *et al.*, 2009), bearing a single layer of enamel overlying dentine tubercles that are resorbed altogether prior to the deposition of a new layer should thus be considered under the 'resorption and deposition' functional view; the ancient explanation of cosmine as a 'sensory' tissue should be avoided. Sensory function might have been assured by other pore-canal systems with larger pores, located mainly in the snout (e.g., see CAMPBELL *et al.*, 2010)

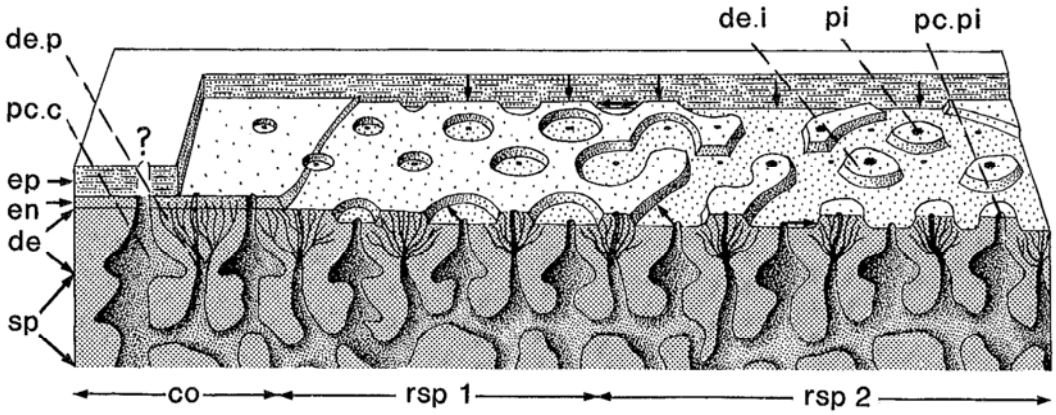



**FIGURE II.1. Reconstruction of the hypothetical process of superficial resorption of a block of cosmine**. The progressive stages of resorption as described by BORGEN (1989) and FOX *et al.* (1995) are as follows. First the enamel layer is removed from a patch on the surface, presumably by the action of the overlying epidermis. Then removal of the dentine layer begins progressively from the inner edge of the area from which the enamel had been removed (rsp1). This progression was marked by an increase in the size of the pores. Such increase in size could be produced by two different processes. The first involves the removal of layers of dentine from the surface by continued action of the epidermis, thus exposing progressively deeper sections through the vertical cavities, giving the impression that the dentine surface was progressively lowered until the mesh canals were exposed (FOX *et al.,* 1995). Alternatively, it could result from resorption of the inner walls of the cavities by osteoclasts housed within them (BORGEN, 1989). The resulting morphology consists of isolated dentine tubercles by the process of fusing of the enlarged pores (rsp2). The probable explanation for the presence of 'pits' in the dentine is that they represent the dentine pulp cavity and/or expanded dentine tubuli that have become exposed because of resorption (BORGEN, 1989). Note that the prolongation of the cosmine pores through a canal in the epidermis (marked with a "?") is merely hypothetical. **Abbreviations: co**, cosmine; **de**, dentine; **de.i**, dentine islets; **de.p**, dentine pulp cavity; **en**, enamel or enameloid; **ep**, external part of the skin comprising epidermis and outer part of the dermis; **pc.c**, pore-canal cavity; **pc.pi**, pit on dentine islet; **pi,** pit on the dentine islets of the 'incomplete resorption'; **rsp 1**, resorption area showing enlarged cosmine pores; **rsp 2**, resorption area showing 'incomplete resorption' zone defined by merging enlarged pores; **sp**, spongiosa (middle vascular bone layer). After BORGEN, 1989.

The hypothesis that the main function of the pore-canal system is to facilitate the deposition and resorption of odontogenic tissues fits into the proposal that an important function of the dermal skeleton is a store for calcium and phosphates (DONOGHUE *et al.*, 2006). The role of cosmine in the metabolic regulation of mineral ions was thoroughly studied by THOMSON (1975) in the megalichthyid "osteolepiform" *Ectosteorhachis* from the Early Permian of Texas, USA, and his conclusions seem very plausible to me. Based on the occurrence of a diverse set of cosmine manifestations (e.g., blisters, tubercles, complete cosmine covering, etc.), THOMSON proposed that such manifestations were due to seasonal resorption of the cosmine in connection with a need to make large volumes of phosphates available, for instance for reproduction, as well as in connection with growth of the dermal skeleton. The ecological correlatives of cosmine resorption suggest that *Ectosteorhachis* may have had an anadromous behavior, and migrated between sea and fresh water to breed. Cosmine resorption would have taken place in fresh water environments, depleted from food resources and minerals compared to the sea.

However, this scenario might be too simplistic when we consider the occurrence of cosmine and cosmine derivatives in other sarcopterygians. Devonian, cosmine-covered sarcopterygians (e.g., stem sarcopterygians, basal onychodontids and actinistians, "porolepidids", dipnoans, and "osteolepidids") seem to be restricted to fully marine environments. (e.g., Spitsbergen, Achanarras, Yunnan sites, etc.). In these forms, cosmine is always well developed and no traces of important resorption due to migrations, as proposed by THOMSON (1975), are seen. These would confirm THOMSON's view that cosmine covering was always continuous in sea environments. However *Cladarosymblema* from the Carboniferous of Australia (FOX *et al.*, 1995) possess a rather continuous cosmine covering and has been referred to a fresh water environment (lacustrine and fluviatile), although important areas of resorption have been observed.

Moreover, possible counter examples are Devonian onychodontids and actinistians, which were strictly marine but appear to have lost cosmine very early in their evolutionary history (FRIEDMAN, 2007a; LU & ZHU, 2010). Nevertheless onychodontids and actinistians, as well as certain holoptychiids, show dentine tubercles capped with enamel; the odontogenic component of the dermoskeleton was thus retained in these marine forms (ØRVIG, 1957).

Curiously, sarcopterygian taxa devoid of cosmine or any other type of odontogenic tissue (e.g., certain holoptychiids, derived dipnoans, rhizodontids, tristichopterids, "elpistostegalians", and tetrapods) have not been found in totally marine environments, but rather in marine-influenced, lagoonal, deltaic, or even freshwater environments (e.g., LEBEDEV & COATES, 1995; JOHANSON & AHLBERG, 2001; CRESSLER *et al.*, 2010). It seems that in these forms, a non-fully marine habitat is related to the loss of odontogenic components of the dermoskeleton. Further studies on these taxa should focus on the paleoenvironment in order to determine if this hypothesis is consistent.

The remaining question is: what could be the advantage of the retention of dentine and enamel (either via cosmine or isolated odontodes) in a marine environment? THOMSON (1975) proposed that dentine was a mean of calcium and phosphate storage in anadromous fishes. Cosmine would be then produced in salt water where these ions are in excess and resorbed in time of short supply or need under certain life conditions, especially when these fishes left the sea to dwell in fresh waters. Resorption processes are highly demanding in energy. Possibly cosmine disappeared convergently in sarcopterygians when certain groups adapted to a more fresh-water environment and found other ways of storing ions without needing to resorb mineral tissues.

Cosmine has proved to be a 'flexible' structure that can be 'easily' resorbed and lead to different configurations (e.g., spoon-shaped tubercles, blisters, Westoll lines, etc.). Resorption is a dynamic process tuned with growth (e.g., cosmine is resorbed along the sutures between dermal bones to be resynthesized once the growth stage has passed). THOMSON's (1975) description of cosmine ontogeny in *Ectosteorhachis* illustrates this point. He proposed that cosmine was laid down around patches of the developing pore-canal mosaic in larval or juvenile fishes. By addition of patches, and after perhaps several episodes of resorption and redeposition as the pore-canal system formed its interconnections, the fish became completely covered with cosmine. In *Ectosteorhachis* then, the pore-canal network and hard tissues apparently developed simultaneously, and later in ontogeny this pattern was altered in various ways, producing discontinuous and mixed cosmine, tubercles, and blisters.

The break up of the cosmine observed in several sarcopterygian groups is considered to have produced vertical canals, communicating the vascular canals of the spongiosa with the exterior. Such canals have been noticed in *Glyptolepis* (ØRVIG, 1956) and similar ones have been described in the gastral scales of *Australerpeton* (DIAS & RICHTER, 2002). However, in tetrapods these are certainly not homologous with the vertical canals of the cosmine pore-canal system, but with openings of the vascular canals of the spongiosa and were probably related to oxygen intake through the scales (WITZMANN *et al.*, 2010). In groups in which early representatives were covered with cosmine, but lost it in derived members (e.g., porolepiforms) these canals can thus considered as remnants of the flask chambers of the cosmine. As previously seen, the function of these cavities is still debated; they have been interpreted as housing electrosensory organs (THOMSON, 1975), osteoclasts (BORGEN, 1988, 1992), dermal papillae supplied by cutaneous blood vessels (BEMIS & NORTHCUTT, 1992) or sites of

mucus-secreting cells (FOX *et al.*, 1995). The canals present in *Glyptolepis* were tentatively interpreted as mucous canals by ØRVIG (1956, fig.5), thus consistent with one of the possible functions of the cosmine cavities.

THOMSON (1975) stated that the presence of a continuous cosmine covering is an ontogenetic character present in reproductive mature individuals. WESTOLL (1936) and WHITE (1965) confirmed the absence of cosmine in small specimens of *Dipterus* and so did ØRVIG (1969a) in small dipnoans indet. from the Devonian of Bergisch-Gladbach, Germany. In *Porolepis* or *Uranolophus*, early generations of odontodes can be seen under the continuous cosmine covering, distributed around the pore-canal cavities (GROSS, 1956; CAMPBELL & BARWICK, 1992). Later in ontogeny, a cosmine sheet was laid down, encasing the pore-canal system and overlying the odontodes that were subject to progressive internal resorption. Cosmine thus develops late in ontogeny. Therefore, the loss of cosmine has been viewed as a paedomorphic trait in sarcopterygian evolution (BEMIS, 1984).

If cosmine formation and structural arrangement of the different tissues composing it are seen as processes subject to heterochronic changes, then the different morphologies resulting from the break up of cosmine present in a variety of sarcopterygian taxa certainly represent changes in the timing of hard tissue and pore-canal development. Moreover, the absence of odontogenic components in some forms (e.g., certain holoptychiids, rhizodontids. tristichopterids, “elpistostegalians”, and tetrapods) could also be correlated with the physiological role of dentine and enamel as storage of mineral ions. An evolutionary tendency can be drawn out from the occurrence and phylogenetic distribution of the cosmine derivatives.

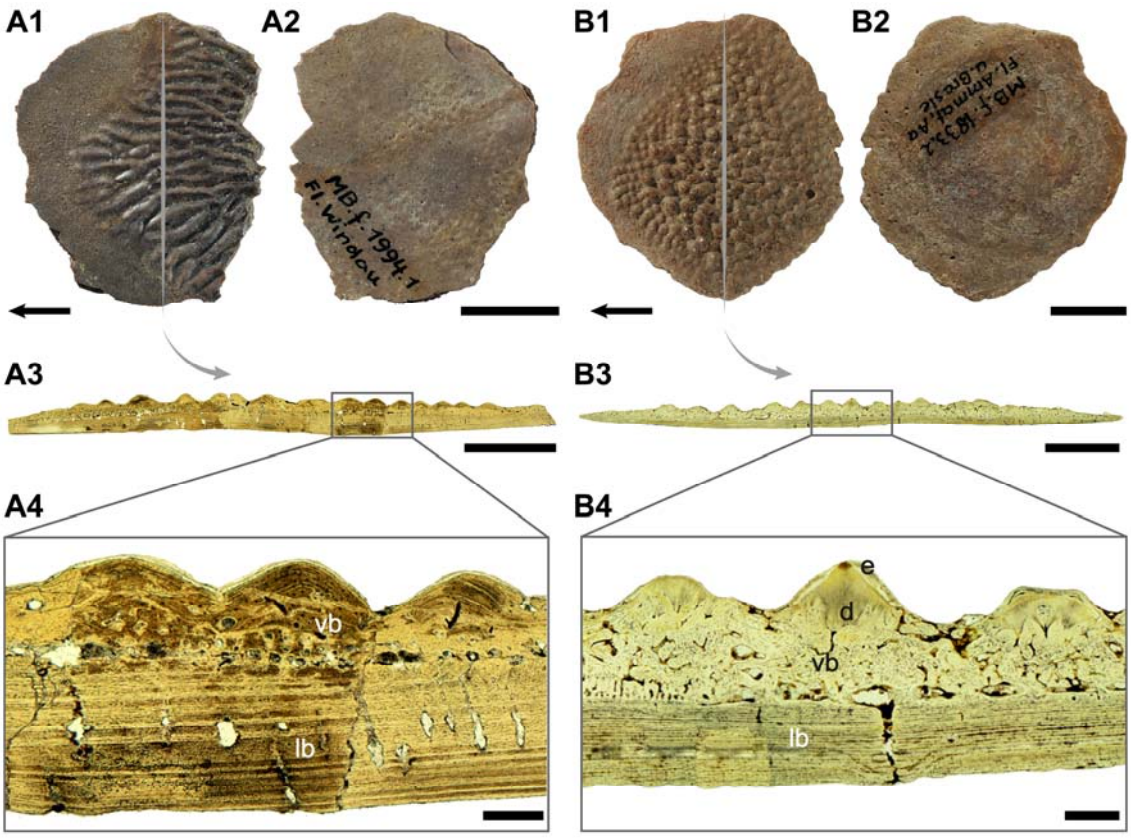



**FIGURE II.2. Morphology and histology of holoptychiid scales A.** *Holoptychius nobilissimus* (MB.f. 1994.1) and **B.** *Laccognathus panderi* (MB.f. 1833,2) from the Late Devonian of Latvia. Cross-sections were made following the dorso-ventral axis of the scales. **1.** External view of the scales (arrow points anteriorly); **2.** Internal view of the scales (scale bar equals 1 cm); **3.** General view of the cross section (scale bar equals 5 mm); **4.** Inset from the cross section showing the arrangement of the histological layers (scale bar equals 500 µm). Note the ornamental and histological differences between both scales: in *Holoptychius* the exposed area is ornamented with thick longitudinal ridges solely made of dense bone resting upon the spongiosa (vascular bone); in *Laccognathus* the exposed area shows numerous dentine tubercles, capped with a thin enamel layer (i.e., odontodes), older odontodes from previous generations are embedded in the underlying spongiosa. In both scales, the internal surface is flat and smooth and is solely formed by the isopedine (lamellar bone) layer, which is relatively thicker in *Holoptychius* than in *Laccognathus*. **Abbreviations**: **d,** dentine; **e**, enamel; **lb**, lamellar bone; **vb**, vascular bone; **vc**, vascular canal.

For instance, in porolepiforms, complete loss of odontogenic components appears to be phylogenetically gradual, with basal members such as "porolepidids" (i.e., *Porolepis* and *Heimenia*) showing a complete cosmine covering. On the other hand, basal holoptychiids, such as *Glyptolepis* and *Laccognathus*, retain a series of superimposed odontodes made of dentine and enamel, whereas *Holoptychius* (consider to be more derived) posses scales completely made of bone, excepting some possible small dentine tubercles anteriorly (Fig. II.2). Moreover, it is possible that *Glyptolepis* could show remnants of the pore-canal system, as proposed by ØRVIG (1956), but histological survey was unfortunately not performed in this thesis in order to confirm or refute it.

In other cosmine-less sarcopterygians, the 'intermediate' stage of retention of odontodes does not occur. Rhizodontids, tristichopterids and "elpistostegalians"+ tetrapods present scales solely made of bone, with no odontogenic contribution to the external ornamentation. Therefore, in these groups the transition from a cosmine-covering condition present in earlier representatives to a full osseous condition in derived members appears to have been 'sudden'. Similarly, this 'switch' seems to be correlated with the transition from the primitive rhombic morphotype, covered with cosmine, to a derived rounded one devoid of cosmine (see below for further details).

An interesting aspect of the histological consequences of the loss of cosmine concerns the fate of the spongiosa, which henceforth becomes exposed as constituting the most external portion of the superficial portion of the scales. THOMSON (1975) stated that in *Ectosteorhachis* the zones of the exposed area devoid of a cosmine covering (either due to more important growth of certain parts of the scale or partial resorption of the cosmine) the naked spongiosa is denser and less vascularised that in normal conditions. Such a dense spongiosa strongly resembles the condition present in the bony scales of *Tulerpeton* (Paper III) and the outer portion of the superficial region of the

scales of *Eusthenopteron* (ZYLBERBERG *et al.*, 2010). However in *Tulerpeton*, the vertical canals of the spongiosa are not present, whereas in *Eusthenopteron* they can occur (ØRVIG *in* JARVIK, 1980). A denser upper part of the spongiosa could have played a role as a reinforcement against mechanical wear of the upper exposed area, or as a way of creating a smoother surface, as seen in the anterior overlapped area, which is solely composed of bone (spongiosa and isopedine), regardless of the scale morphotype and the histological structure of the exposed area.

In relation to wear, a common explanation to the distribution of cosmine deals with the role of cosmine as a sort of 'shield' in parts of the body that could have been more exposed to contact with substrate (CLÉMENT, 2004). Now that I have showed that the sensory role of cosmine should not be taken for granted, the role of cosmine as a protective 'armour' should also be reconsidered. We should not forget that in all fishes the dermal skeleton is not 'naked', or totally exposed to the environment. The bones of the skull, fins, and scales are overlain by the epidermis, which in the vast majority of cases produces a mucus improving water penetration and minimizing injuries caused by rough substrate contact. Even if cosmine appears to be more developed in the ventral region of the body and anterior portion of the snout in certain taxa (e.g., *Porolepis*, *Heimenia*, dipnoans, etc.), it does not necessarily mean that these regions were more 'protected' from injuries by the presence of cosmine. The skin, which is a living tissue with nervous connections, would have been continuously wounded, producing not only pain to the animal, but also implicating a regular healing, which is an energy-consuming process. I propose instead that the presence of 'thicker' cosmine in these regions could have had a role in increasing the weight of the ventral region and the anterior tip of the snout in benthic fishes as a resistance against buoyancy and therefore, facilitating swimming.

Finally, and unfortunately, given the current knowledge on dermoskeleton development in early vertebrates and the sarcopterygian material at hand, it is not possible to arrive at a definite answer as to how the cosmine system truly formed and functioned.

**RUSSIAN "OSTEOLEPIFORMS"** – Recently, FRIEDMAN in COATES & FRIEDMAN (2010) reviewed the Late Devonian "osteolepiforms" *Thysanolepis* and *Vorobjevaia* from Russia housed in the PIN, Moscow. Based on his observations, FRIEDMAN stated that both genera were "probable rhizodonts" (COATES & FRIEDMAN, 2010: 402). Histological cross sections at my disposal, furnished by François MEUNIER at the beginning of my thesis, comprised three Russian tetrapodomorphs: *Thysanolepis*, *Lamprotolepis* (VOROBYEVA, 1977b) and *Megistolepis* (OBRUCHEV, 1955). In these cross sections (Fig. II.3) I could identify the different histological layers of the cosmoid scales (in *Thysanolepis* and *Megistolepis*) as present in basal sarcopterygians and similar to the cosmine of "osteolepiforms" (e.g., *Megalichthys*), and the presence of dentine tubercles in *Lamprotolepis,* similar to the holoptychiid condition (e.g., *Laccognathus,* fig. II.2.B). However, as proposed by FRIEDMAN, *Thysanolepis* would be a putative rhizodontid. As seen in Fig. II.3.C, cosmine is present and well developed in the scales of *Thysanolepis*.

Cosmine is not known in any rhizodontid, not even in the basal most representative *Gooloogongia* (JOHANSON & AHLBERG, 1998). Rhizodontids have rounded scales ornamented by bony ridges in their external surface, very similar to those of tristichopterids, but certainly acquired by convergence (AHLBERG & JOHANSON, 1998). If future phylogenetic analyses confirm FRIEDMAN's supposition about its rhizodontid nature, *Thysanolepis* would constitute the first cosmine-covered rhizodontid, and would probably be placed as the sister group of all other rhizodontids.

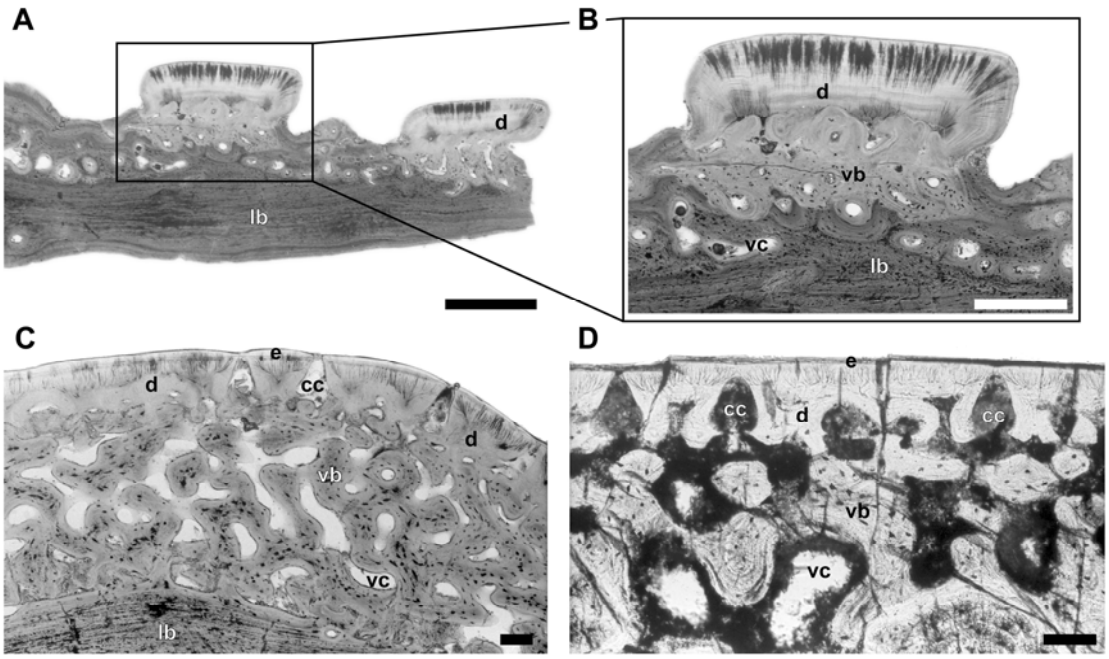



**FIGURE II.3. Histological cross sections of Russian tetrapodomorph scale material. A**. *Lamprotolepis* ("Osteolepiformes"), fragment of a scale ornamented with dentine tubercles. Scale bar equals 1 mm. **B.** Inset of a tubercle (odontode). Note the absence of cosmine and of enamel capping the dentine tubercle. The odontodes lie on a thin and irregularly developed layer of vascular bone (spongiosa). The basal lamellar bone layer (isopedine) is thick and well developed. Scale bar equals 500 µm. **C.** *Thysanolepis* (?Rhizodontida), upper portion of a scale in cross section. Note the presence of cosmine formed by the association of enamel and dentine pervaded by a pore-canal system. The middle vascular bone layer is well developed and rest on the isopedine basal layer. Scale bar equals 100 µm. **D.** *Megistolepis* ("Osteolepiformes"), upper portion of a scale in cross section. Note the presence cosmine and a well developed and cancellous spongiosa. The inferior part of the pore-canal system of the cosmine prolong itself into the vascular canals of the spongiosa. Basal layer not visible. Scale bar equals 100 µm. **Abbreviations**: **cc**, cosmine canal; **d,** dentine; **e**, enamel; **lb**, lamellar bone; **vb**, vascular bone; **vc**, vascular canal. Pictures courtesy of François MEUNIER.

In this case, the loss of the cosmine in the rhizodontid lineage from cosmine-covered basal members would constitute another example of the convergent loss of the cosmine in Devonian sarcopterygians (as in onychodontids, actinistians, porolepiforms, dipnoans, and "osteolepiforms"). It is still too soon to make such assertions, but thorough revision of the Russian sarcopterygian faunas is greatly needed.

***GLYPTOPOMUS AND PLATYCEPHALICHTHYS* OR THE "ELPISTOSTEGALIANS" REVISITED** – *Glyptopomus* is a puzzling tetrapodomorph genus known from the Famennian of Scotland (Rosebrae Beds and Dura Den; JARVIK 1950), but also reported from Pennsylvania (NEWBERRY, 1889), and central Russia (LEBEDEV, 1995b). *Glyptopomus* comprise four species: *G. minor* AGASSIZ, 1844, *G. kinnardi* HUXLEY, 1859, *G. sayrei* NEWBERRY, 1878, and *G. elginensis* JARVIK, 1950. A putative fifth species, *G. ?bystrowi* GROSS, 1941, is solely known from disarticulated scales material and thus should not be confidently assigned to a new species.

The study of published material and anatomical descriptions of *Glyptopomus* has led me to think that *Glyptopomus* might lie closer to tetrapods than previously thought. If my suppositions are correct, *Glyptopomus* should no longer be considered a generalized "osteolepiform", but rather a stem "elpistostegalian". These assumptions are mainly supported by the morphology and histology of the scales and by the median fin pattern.

In his study of the "osteolepiforms" from Scotland, JARVIK (1950) stated that *G. minor* and *G. kinnairdi* possessed a diphycercal caudal fin, with a rhomboidal outline. *G. sayrei* and *G. elginensis* are incompletely known and their caudal fin are not preserved (NEWBERRY, 1889), although it is very likely that they also had a diphycercal tail (HUXLEY, 1861; JARVIK, 1950).

The scales of *Glyptopomus* are rhombic in shape but lack cosmine. This condition is known in certain rhizodopsid "osteolepiforms" (e.g., *Rhizodopsis*) (SCHULTZE & HEIDTKE, 1986), *Litoptychus* (DENISON, 1951b; COATES & FRIEDMAN, 2010), and in "elpistostegalians" (e.g., *Panderichthys* and *Tiktaalik*) (WITZMANN, 2011). Moreover, the scales are ornamented by a series of bony tubercles and small ridges, similar to the condition of "elpistostegalians". JARVIK (1950) also described the absence of dermal scutes at the base of the fins, a condition characteristic of tristichopterids (e.g., *Eusthenopteron*), and the presence of a large epichordal lobe in the diphycercal caudal fin of *G. kinnairdi*. These two characters are shared with *Panderichthys* and tetrapods, suggesting that *Glyptopomus* might fall crownward of tristichopterids.

The gross morphology of *Glyptopomus* closely resembles that of *Gyroptychius*, another "osteolepiform" from the Late Devonian of Scotland (JARVIK, 1985). Both genera have two posteriorly located dorsal fins, a diphycercal caudal fin, and rhombic scales. However, the scales of *Gyroptychius* show a cosmine covering. Moreover, JARVIK (1985) pointed out that, compared to the symmetrical condition of the lobes of the caudal fin in *Gyroptychius*, the dorsal lobe of the caudal fin in *Glyptopomus* seems to be as high as or higher than the ventral one. This is at odds with the common condition of "osteolepiforms" in which the ventral lobe is always more developed and carries more lepidotrichia than the dorsal one, even in the case of diphycercal caudal fin as in tristichopterids. THOMSON and HAHN (1969) proposed that this condition was a reminiscence of the well-developed ventral lobe of the heterocercal tail of basal "osteolepiforms" (e.g., *Osteolepis*) (JARVIK, 1944). However, in "elpistostegalians" and tetrapods with diphycercal caudal fins, the dorsal lobe is always more developed and spreads more anteriorly than the ventral one (VOROBYEVA & SCHULTZE, 1991; COATES, 1996), thus inverting the scenario proposed for "osteolepiforms" by THOMSON and HAHN.

The phylogenetic position of *Glyptopomus* is unknown since, to my knowledge, no phylogenetic study has included *Glyptopomus* in the data set. SCHULTZE and CHORN (1998) suggested a close relationship between *Litoptychus,* megalichthyid "osteolepiforms", and *Glyptopomus,* but recently COATES and FRIEDMAN (2010) ruled it out. The derived characters claimed to link *Glyptopomus* and *Litoptychus,* such as the absence of cosmine and the presence of a dentary fang, are viewed as convergent. COATES & FRIEDMAN (2010) located *Litoptychus* in a large cluster of megalichthyforms (i.e., as the clade comprising all taxa more closely related to *Megalichthys* than *Eusthenopteron*) and proposed that *Glyptopomus* would lie close to or within the clade comprising tristichopterids, "elpistostegalians", and tetrapods. Indeed, the absence of cosmine and the presence of a dentary fang are features also found in members of this radiation of derived tetrapodomorphs (see Paper VI).

The absence of cosmine is insufficient to assign a position to *Glyptopomus* within crownward tetrapodomorphs since it has been lost at least in five lineages within the Tetrapodomorpha (e.g., rhizodontids, tristichopterids, some canowindrids and rhizodopsid "osteolepiforms", and "elpistostegalians"+tetrapods). The presence of dentary fangs is also highly convergent, being know in rhizodontids, derived tristichopterids, "elpistostegalians", and tetrapods. However, the caudal fin shape and arrangement of the lepidotrichia is closer to the condition seen in "elpistostegalians" and tetrapods than in any other tetrapodomorph fish, with the exception of *Gyroptychius*. These three characters put together give a glimpse of a putative phylogenetic position of *Glyptopomus*. If we consider that *Gyroptychius* and *Glyptopomus* are closely related, the presence of cosmine in *Gyroptychius* places it below tristichopterids (e.g., AHLBERG & JOHANSON, 1998). On the other hand, the absence of cosmine, despite being highly convergent, plus the occurrence of dentary fangs and a

well-developed diphycercal tail, would locate *Glyptopomus* crownward to tristichopterids, thus among the stem Elpistostegalia (*sensu* DAESCHLER *et al*., 2006). Scale histology is a strong argument in favour of the position of *Glyptopomus* as stem "elpistostegalian", the bony ornamentation of the external surface of the scales as figured by JARVIK (1950) is extremely similar to that of *Panderichthys*, *Tiktaalik* and *Elpistostege* (SCHULTZE, 1996; WITZMANN, 2011, *pers. obs*.).

An almost identical situation was also highlighted by COATES and FRIEDMAN (2010) for *Platycephalichthys*, which is certainly a polyphyletic genus. Of the two species currently comprised in the genus *Platycephlichthys*, *P. skuenicus* posses rounded scales and could be located among tristichopterids, whereas *P. bischoffi* shows rhombic scales without cosmine and thus might be closer to "elpistostegalians" (CLÉMENT 2002; SNITTING 2008b). In any case, thorough studies of *Glyptopomus* and *Platycephalichthys* are needed. The inclusion of histological features among other more 'classic' anatomical characters could shed more light on the phylogenetic relationships of these two genera and bring new data on the histological and morphological transformations between "osteolepiforms" and the clade comprising "elpistostegalians" and tetrapods.

## III. TRANSITION FROM RHOMBIC TO ROUNDED SCALE MORPHOTYPE

As stated in Paper I, evolutionary transitions of the squamation from rhombic to rounded scales have occurred independently in actinopterygians (SCHULTZE, 1966, 1977, 1996; PEARSON, 1982) and sarcopterygians (ØRVIG, 1957; SCHULTZE, 1969b; JARVIK, 1985). As seen in the previous section, the physiological role of the odontogenic tissues in the scales is related to morphological and ornamentation variations in the squamation (e.g., break up of the cosmine). However, in this section I will discuss the morphofunctional importance of the squamation and its relationship with developmental and evolutionary changes. Therefore, my starting hypothesis is that the evolution of squamation in fishes is dependent on two main factors: physiology and functional morphology.

The first issue I would like to point out is the transition between scale morphotypes during ontogenetic development. Rounded shape is typical for very early stages of scale formation in fish ontogeny, surely before dermal ossification takes place. In the larvae of the rhombic-scaled actinopterygian *Polypterus* the scales are rounded in shape (BEMIS, 1984, fig.7a). However, BARTSCH *et al.* (1997, fig.20) showed that they soon become rhombic as they start ossifying. When working with fossil specimens, we do not have access to early phases of the development; larval stages are very rare, except in some extraordinary cases (CLOUTIER, 2010). Moreover, scales are only found in fossil specimens when they are ossified enough as to be preserved (COTE *et al.*, 2002). In sarcopterygians, rhombic and/or rounded scales usually show the same general outline in juvenile ontogenetic stages as in the adults (e.g., the rounded scales in juvenile specimens of *Holoptychius*, CLOUTIER & SCHULTZE, 1996, fig. 9) except in cases where allometric growth modifies the scale outline during ontogeny (e.g., *Tulerpeton*, Paper III).

Modification of the scale morphology has been usually attributed to heterochronic changes (e.g., PEARSON, 1982; CHEN, 2010). I already stated that the loss of cosmine is considered a paedomorphic trait in sarcopterygians. Therefore, since the earliest ontogenetic morphotype seen during normal fish development appears to be the rounded one, it is therefore possible that rhombic shape might correspond to a peramorphic trait, whereas rounded shape might be seen as paedomorphic. Moreover, it could also be stated that a transition from and/or the combined occurrence of rhombic and rounded scale morphotypes in a single individual (e.g., *Heimenia* and other examples presented in Paper I) represents an epigenetic process during the ontogeny in which certain scales acquire a more 'mature' state than others.

Along with heterochronic processes, our understanding of the morphofunctional implications of fish anatomy depends on the study of scale shape, 'peg-and-socket' articulation, scale attachment devices, etc. Morphofunctional implications of the squamation in fishes are well known (e.g., LINDSEY, 1978; BURDAK, 1979; GEMBALLA & BARTSCH, 2002) and evolutionary scenarii can be proposed with relative confidence based on the differences in pattern, outline, and articulation devices between scale morphotypes in different lineages of osteichthyans.

For instance, in the case of *Heimenia*, the regionalization of the squamation into a rhombic-scaled posterior region and a rounded-scaled anterior region might not only evidence epigenetic modifications of the scale shape during ontogeny, but it may also be dependent on the morphofunctional characteristics and constraints of both scale morphotypes. The study by GEMBALLA and BARTSCH (2002) on the functional morphology of the rhombic squamation of polypterids and lepisosteids showed that a rhombic squamation is not necessarily more impeding for body bending than a rounded one. The authors argued that the limit of body flexion was never reached during steady

swimming in these fishes. Moreover, they demonstrated that a rhombic squamation is somehow 'suitable' to allow extreme body curvatures. However, due to the occurrence of a 'peg-and-socket' articulation and the well-developed innervation of the articular ridges by Sharpey's fibers in the scales of these forms, bending of the body can only occur along the lateral axis; dorso-ventral axis bending is impeded by the very characteristics of the articulation features of the rhombic squamation.

GEMBALLA and BARTSCH (2002) also established that the posterior half of the body is subject to great torsion in torpedo-like fishes (such as *Lepisosteus* and *Polypterus*). The same scenario can be applied to certain sarcopterygians (e.g., porolepiforms, "osteolepiforms", and possibly even "elpistostegalians" to a certain extent). In these fishes, the caudal fin provides the main locomotory thrust and dorsal fins (when present) are displaced posteriorly. In rhombic-scaled porolepiforms and "osteolepiforms", the rhombic squamation would have suited the enhancing of body torsion, especially in the caudal region. Indeed, as PEARSON (1982) pointed out, the early members of each major group of osteichthyans usually possess an elongate body. PEARSON also proposed that an elongate-fusiform body shape, along with a rhombic squamation, was probably related to the 'ancestral' swimming mode. In the case of *Heimenia*, the maintenance of rhombic scales in the posterior half of the body and along the caudal peduncle is consistent with the adaptive qualities of rhombic squamation to torsion in carangiform to subcarangiform swimming styles (BELLES-ISLES, 1992) (Fig. III.1). As proposed in Paper I, the occurrence in *Heimenia* of rounded scales in the anterior half of the body could be related to more diverse set of movements of the region immediately behind the head, allowing the trunk to move along more axes than solely laterally, as opposed to the posterior region. The same scenario could be applied to other osteichthyans in which both scales morphotypes are present (e.g., *Thunnus*).

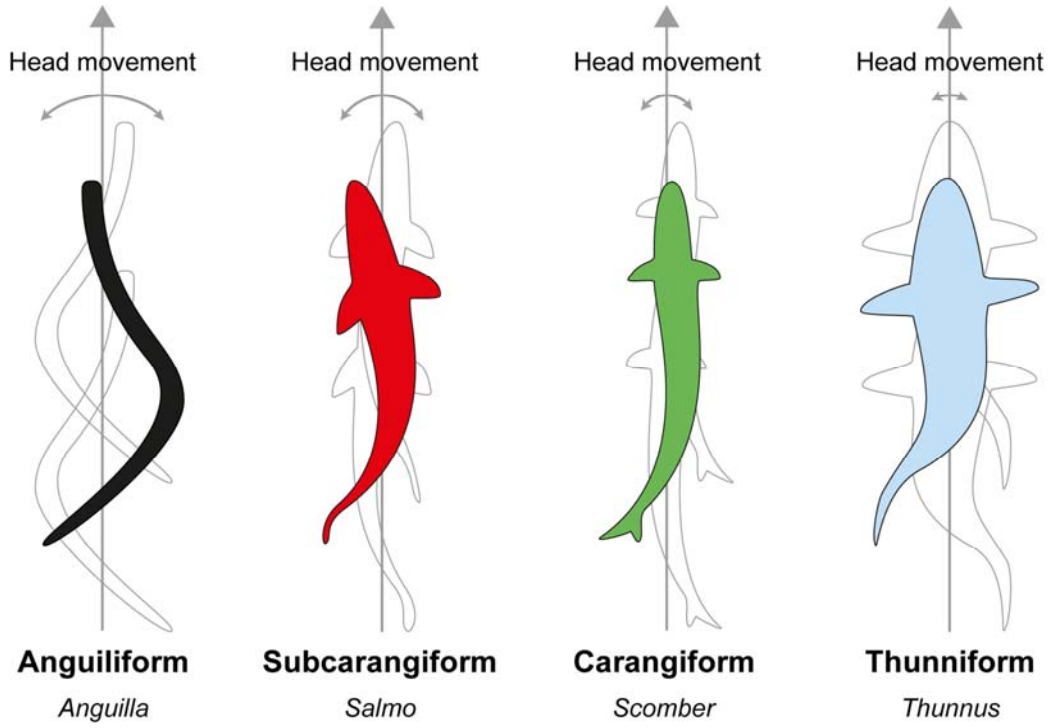



**FIGURE III.1. Swimming modes in fishes. Anguilliform** swimming is a purely undulatory mode of swimming, in which most or all of the length of the body participates. **Subcarangiform** swimming is similar to anguilliform, but differs in the latter in a steadier anterior portion of the body and a more flexible caudal fin. In **carangiform** swimming, undulations are confined to the posterior-most third of the body, which is capable of wide flexure, and thrust is delivered by a stiff caudal fin. In **thunniform** swimming, the thrust is generated exclusively by a high stiff caudal fin mounted on an extremely narrow peduncle. Significant lateral movement occurs only in the peduncle and tail. Redrawn after LINDSEY, 1978.

The ancestral rhomboid scale of osteichthyans is characterized by the occurrence in the narrow anterior and dorsal overlapped areas of articulations devices in the shape of processes. The first evidence of such processes appear in *Naxilepis*, a stem osteichthyan from the Silurian of China (WANG & DONG, 1989; FRIEDMAN & BRAZEAU, 2010). *Naxilepis* shows an anterodorsal process, a condition common to several stem osteicththyans, sarcopterygians and actinopterygians (e.g., *Dialipina, Guiyu*, *Psarolepis, Mimia*, *Moythomasia*) (GARDINER, 1984; SCHULTZE, 1968, 1992; ZHU *et al.*, 2009). However,

the most common condition in early sarcopterygians and actinopterygians is the dorsal 'peg'. Anterodorsal process and narrow 'pegs', as well as ganoid and basal fulcra, were considered as synapomorphies of actinopterygians (PATTERSON, 1982, GARDINER, 1984; JANVIER, 1996). However, anterodorsal processes are also notable in stem sarcopterygians (e.g., *Guiyu*, *Psarolepis; Styloichthys*) (ZHU *et al.*, 2009; CHEN, 2010). Pointed 'pegs' also occur in sarcopterygians (e.g., *Youngolepis*, *Uranolophus*, *Dipnorhynchus, Powichthys, Arquatichthys, Porolepis*, *Heimenia*, *Osteolepis*) (GROSS, 1966; DENISON, 1968; JARVIK, 1980; CAMPBELL & BARWICK, 1988; ZHU & FAN, 1995; CLÉMENT & JANVIER, 2004; LU & ZHU, 2008; Paper I). The 'classical' distinction between the primitive rhomboid actinopterygian and sarcopterygian scales has become blurred by the discovery of certain stem sarcopterygians and osteichthyans (Fig. III.2).

In addition to the anterodorsal process and dorsal 'pegs', a second process occurs in the anterior portion of the overlapped area in some sarcopterygians. These processes can coexist and anteroventral processes are clearly present in *Powichthys, Youngolepis,* and *Arquatichthys* (CLÉMENT & JANVIER, 2004; LU & ZHU, 2008). *Kenichthys* possesses a much less pronounced anteroventral process (CHANG & ZHU, 1993), and certain rhombic and intermediate scales of *Heimenia* show possible remnants of such a process (Paper I). The loss of these two processes in different sarcopterygian groups (e.g., actinistians, onychodontids, porolepiforms, dipnoans and most tetrapodomorphs) might represent a case of parallel evolution. Moreover, it has become clear that the 'peg' of the overlapped external surface is intrinsically linked to the 'socket' of the internal surface in such way that the absence of a 'peg' mechanically leads to the absence of a socket, and hence to a smooth internal surface of the scale.

Anterodorsal processes limit the lateral flexibility of the trunk (GEMBALLA & BARTSCH, 2002), and as previously seen, the 'peg-and-socket' articulation impedes dorso-

ventral flexion during swimming. Moreover, a rhombic squamation can be considered as 'flexible' only when overlapping surfaces are reduced (e.g., the ganoid rhombic squamation of *Polypterus* and *Lepisosteus*). On the other hand, large overlapping areas are not related with flexibility, on the contrary they strengthen the trunk constraining lateral flexion (PRIDMORE & BARWICK, 1993). These can explain the narrow overlapped areas in the rhombic scales of early osteichthyans, and the convergent loss of antero-dorsal and antero-ventral processes in actinopterygians and sarcopterygians. Therefore the architecture of the ancestral rhombic squamation evolved in parallel in both osteichthyan lineages, probably as an adaption to new more dynamic behaviours that could have been somehow restricted in earlier members of both clades. Curiously, in the vast majority of cases, rhombic scales were replaced by rounded scales, which constitute an extreme simplification of the articulation devices of the general scale outline.

Concerning the usual occurrence of cosmine in rhombic scales, the condition of *Heimenia* constitutes a remarkable exception among sarcopterygians. It has become rather assumed that cosmine can only be found in rhombic scales. The evidences in favour of this are numerous (e.g., ØRVIG, 1957, 1969a,b; JARVIK, 1985; LU & ZHU, 2008). However, the case of *Heimenia* and *Dipterus* (*pers. obs*.) shows that rounded shape of the scales evolved first; the loss of cosmine is secondary and there seems to be no direct correlation between a rhomboid shape and the presence of cosmine, at least in dipnomorphs. These examples suggest that cosmine is thus not necessarily restricted to the rhombic scales. On the other hand, rhombic scales without odontogenic contribution (i.e., cosmine, ganoine, and/or dentine tubercles) solely occur in sarcopterygians (e.g., the "osteolepiforms" *Litoptychus, "Platycephalichthys"* and *Glyptopomus,* and "elpistostegalians"). To my knowledge, actinopterygian rhombic scales are always covered by ganoine.

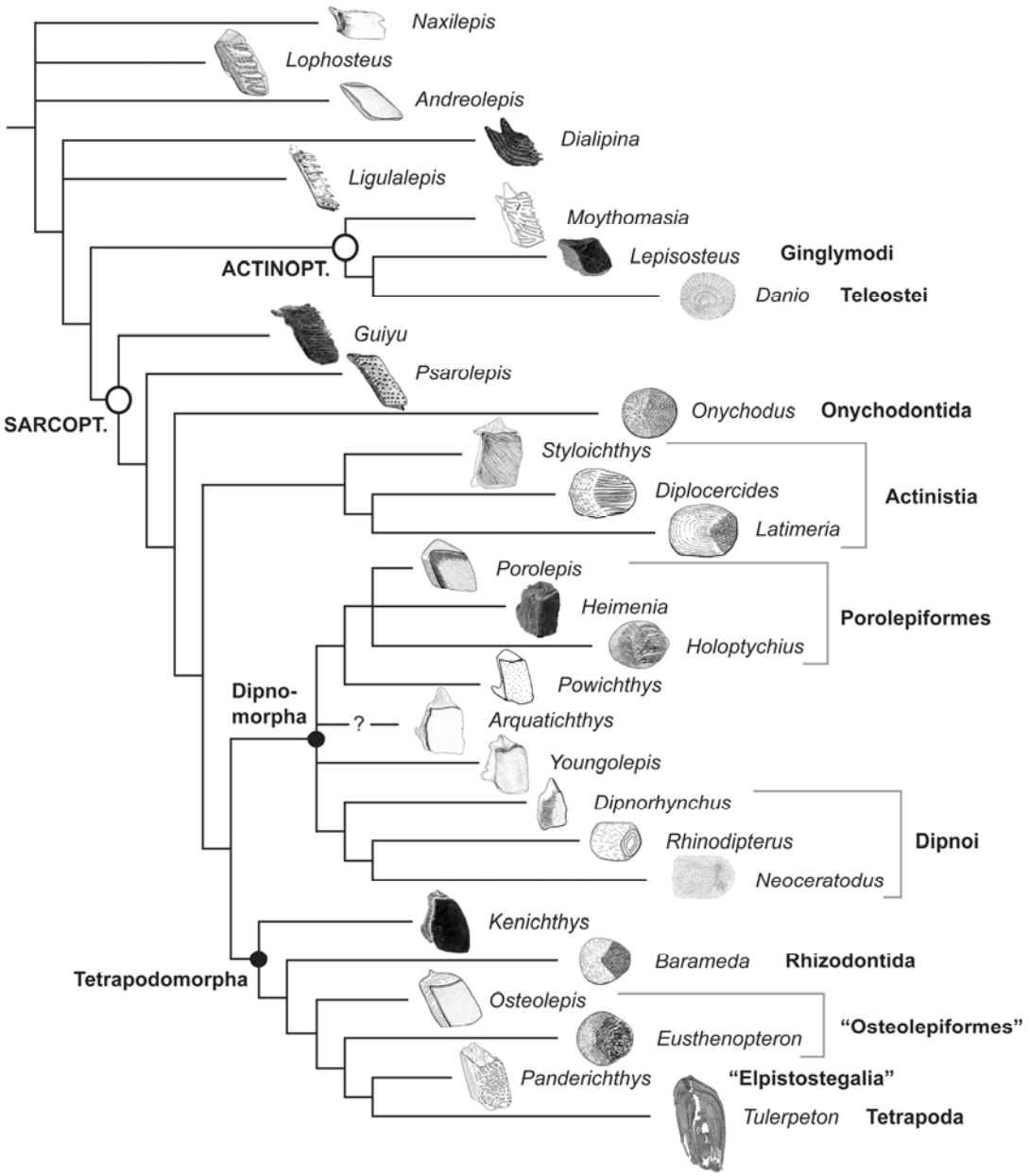



**FIGURE III.2. Squamation evolution in osteichthyans.** The primitive condition of the osteichthyan squamation is probably the presence of articulation processes (antero-dorsal process and dorsal 'peg') in the narrow overlapped area of rhomboid scales. These processes are independently lost in several lineages along with the acquisition of a rounded outline with large overlapped areas and the reduction or loss of odontogenic tissues. Stem osteichthyan and dipnomorph phylogenetic hypothesis after FRIEDMAN & BRAZEAU, 2010; LU & ZHU, 2008, respectively. Drawings and pictures after BRIEN, 1968; JARVIK, 1980; GARDINER, 1984; CHANG & ZHU, 1995; JANVIER, 1996; CLÉMENT & JANVIER, 2004; ZHU *et al.*, 2009; CHEN, 2010; WITZMANN, 2011; Paper I, III.

A singular feature of the scales of sarcopterygians is the presence of tubercles (made either of bone or dentine, sometimes capped with enamel) at the edge of the overlapped and exposed regions. The distribution of these tubercles is always similar in all groups: they can be found in the antero-dorsal margin of the cosmine in rhombic or rounded scales, and in the exposed area arranged like beads that can anostomose and form parallel ridges to the antero-posterior axis of the scale. Both distributions are related to morphofunctional purposes of the tubercles: anterior ones are involved in adhesion of the scale to the epidermis (BURDAK, 1979) and those of the exposed area control and direct the water flow. However, anterior tubercles can be absent form certain groups that present large, rounded scales (i.e., holoptychiids, rhizodontids and tristichopterids). In these cases it seems that adhesion has been neglected against to control of the water flow mediated by the bony ridges. Indeed, water flow control is essential, and thus tubercle and/or ridge ornamentation in the exposed area is a rather constant condition in the rounded scales of sarcopterygians.

When considering the major differences between rhombic and rounded scales in sarcopterygians, the fate of the oblique articular ridge of the internal surface of the rhombic scales played a major role in the morphofunctional differences between both scale morphotypes. The internal keel is considered as an addition to the basal layer that clearly does not form like the isopedine (MEUNIER, 1987, 2011). Therefore, it becomes relatively 'easy' to assert that its loss can occur independently in several groups (e.g., holoptychiids, dipnoans, *Litoptychus*). In *Heimenia*, the bony tissue of the keel is maintained in rounded scales covered with cosmine. The keel is a morphofunctional structure of the basal portion of the scale dependent on the constraints of scale shape and locomotion, but it does not seem to be dependent on the development or histological structure of the superficial layers (e.g., the presence of cosmine or ganoine).

Indeed, rhombic scales without cosmine still possess a keel, as in "elpistostegalians" (e.g., *Panderichthys* and *Tiktaalik*). The keel seems thus linked to the rhombic shape of the scales, but curiously the bony tissue forming the keel is maintained in taxa that show rounded scales (e.g., in *Heimenia* where it spreads along the internal surface, and in rhizodontids and tristichopterids where it forms the internal drop shaped boss).

The independent acquisition of a rounded morphotype is a clear example of convergence in the evolution of osteichthyans. As evidenced in *Heimenia* (Paper I) the acquisition of a rounded morphotype is linked to a more pronounced growth of the anterior overlapped area, such as the anterior margin of the scales becomes rounded *before* the posterior one. THOMSON (1975) also indicated that in *Ectosteorhachis* the posterior margin of the scales always shows continuous and finished cosmine rims. However, the anterior portion of the cosmine does not reach the anterior groove in certain large scales, implying that the anterior portion of the scale has grown more importantly and that cosmine had not yet spread anteriorly to cover this naked exposed region of the spongiosa. This condition is similar to the pattern seen in *Heimenia* in which the anterior overlapped areas are proportionally larger in the rounded scales than in the rhombic ones. The same is true for all other osteichthyans (Fig. III.2). Moreover, THOMSON (1975) described the scales of *Ectosteorhachis* as thinner and more rounded than those of other cosmine-covered "osteolepidids"; the growth of the anterior portion also appears to be correlated with a less marked internal articular ridge (keel) and a rounded outline. The same condition is present in *Heimenia*.

Finally, the enhancement or reduction of the microstructural and morphofunctional features during the evolution of the squamation might simply be due to developmental heterochronic modifications in the formation of the scales. Allometric differences in growth rate of certain portions of the scales are ontogenetic-related

process. Prolongation or delay of growth can be easily matched with different scale morphologies as seen in osteichthyans (e.g., a prolonged growth is responsible for a more rounded outline, whereas early cessation of growth is characteristic of rhombic scales). I didn't have the time during my thesis to explore the genetic basis for the morphological changes of the squamation. Further experimental studies should focus on the role of certain molecules (e.g., Eda, Shh, etc.) related with growth and pattern of dermal components, such as scales (e.g., MONNOT *et al.*, 1999; SIRE & AKIMENKO, 2004; HARRIS *et al.*, 2009; SCHMID & SÁNCHEZ-VILLAGRA, 2010).

## IV. SQUAMATION EVOLUTION IN TETRAPODS

As reviewed in Paper III, the idea that dermal scales were extensively lost during the origin of tetrapods (excepting the ventral 'gastral' scales that might have derive into the gastralia of amniotes), is largely overstated and is probably due to the comparison of early tetrapods with extant lissamphibians (excepting gymnophionans) that do not posses dermal scales. Many groups of Carboniferous tetrapods (e.g., temnospondyls, embolomeres, lepospondyls) retained dermal scales with different degrees of mineralisation and distribution along the body (CARROLL, 1992), with scales located ventrally as well as dorsally.

The apparent lack of a well-developed squamation in Devonian tetrapods, albeit the numerous ventral scales preserved in *Acanthostega* (COATES, 1996) and the putative tail scales of *Ichthyostega* (JARVIK, 1996), led CLACK (2002a) to suggest that dorsal scales were completely lost in Devonian tetrapods. The presence of dorsal dermal scales in Carboniferous tetrapods were thus due to a secondary recovery (CLACK, 2002a:172). It is known that the integument is a flexible tissue capable of producing a large set of skeletal derivatives in tetrapods (VICKARYOUS *et al.*, 2009) and it has been shown that in fishes and other vertebrates the dermis has the potential for producing independently skeletal derivatives (e.g., ZYLBERBERG & WAKE, 1990). The dermis has thus an inherent capacity of producing osseous elements in separate groups without implying close relationship (as proposed for the presence of dermal scales in gymnophionans, ZYLBERBERG & WAKE, 1990).

The possibility that the dermal scales of *Tulerpeton* could have retained an unmineralized isopedine layer as in extant sarcopterygians (e.g., *Neoceratodus* and *Latimeria*) led me to think that dorsal scales of early tetrapods might have been less

mineralized than the ventral (gastral) ones, and hence they were less likely to be preserved and found in fossil specimens. The presence of ossified ventral and dorsal scales in Carboniferous tetrapods (e.g., *Dendrerpeton*, *Proterogyrinus*) (MILLER, 1980) might suggest that dorsal scales were not completely lost in Devonian tetrapods and secondarily recovered after the Devonian as previously considered (CLACK, 2002), but rather that well ossified dorsal scales of temnospondyls regained an important osseous component that enabled them to be easily preserved in fossil specimens. As CARROLL (1969) pointed out, in other Palaeozoic tetrapods such as "romeriids", limnoscelids or "pelycosaurs" the dorsal scales are not found ossified, thus implying that they should have certainly been present but due to their light ossification rate they were not preserved in fossil specimens. This scenario is consistent with the variable ossification capacities of the integument and with the similarities in histological microstructure of the ventral and dorsal scales between Devonian taxa (e.g., *Tulerpeton*) and Carboniferous temnospondyls (e.g., *Plagiosuchus*) (WITZMANN, 2011; Paper III).

The differential ossification rate between dorsal and gastral scales is informative of the importance of gastral scales in visceral support in the earliest tetrapods. As previously considered, *Acanthostega* and *Ichthyostega* could have left the water for short intervals of time and hence supporting structures such as gastral scales could have been useful during their land incursions when their bellies were resting on the ground. The condition of *Ichthyostega* exemplifies this proposed scenario: spindle-shaped gastral scales have recently been identified (CLACK *in* DAESCHLER *et al.*, 2009) but dorsal scales are restricted to very light impressions in the caudal fin, covering the radials and the proximal portion of the caudal lepidotrichia. However, CLACK casted doubt in these scales as published by JARVIK (1996:pl. 37, 38, 39) and suggested that they could be some

reflection of soft tissue replaced by a different matrix (CLACK, *pers. comm*., 2012). A detailed examination of caudal specimens of *Ichthyostega* will certainly settle this issue.

Another important issue concerning the presence or absence of dorsal scales in Devonian tetrapods deals with the conditions of preservation and fossilization of taxa. The holotype of *Tulerpeton* seems to have been preserved *in situ*; postmortem disruption of the material is attributed to bacterial action and decay gases rather than scavenging, transportation appears to have been minimal, and subaqueous maceration fast and efficient (LEBEDEV & COATES, 1995). On the other hand, Greenland tetrapods (*Acanthostega* and *Ichthyostega*) appear to have been subject to a certain degree of transport before fossilization since deposition is considered to have occurred as a rapid accumulation of animal remains with many individuals deposited together, perhaps after a flash flood (CLACK, 2000). The scales of *Tulerpeton*, preserved in a shallow, low energy environment are thus more commonly preserved than those of *Acanthostega* and *Ichthyostega,* which remains were abruptly transported before burial. Scales, being the most external and most loosely attached skeletal elements are thus more likely to be lost in case of sudden floods, especially if the animals were already dead. Similarly, the fact that dorsal and flank scales are more often preserved in Carboniferous tetrapods could simply be due to the occurrence of more suitable fossilization conditions during the Carboniferous than during the Devonian.

However, the dorsal scales show a marked evolutionary trend in tetrapod evolution during which scale overlapping is loss in many groups along with the subsequent complete loss of dorsal scales. This has been attributed to the enhancement of skin respiration that was accordingly more important in Palaeozoic tetrapods with a reduced scale covering (ROMER, 1972). Moreover, Devonian and Carboniferous tetrapods were mainly aquatic animals; contact of the skin with the air interface would have

occurred mainly through the dorsal and trunk regions of the body and little in the ventral region. Accordingly we see that the loss of scale overlapping, and hence the enhancing of skin respiration, occurred mainly in the dorsal and trunk surfaces. The gastral scales maintained their overlapping pattern to fulfil their role of protection from compression of the viscera with the substrate.

Carboniferous tetrapods show a rearrangement of the ventral squamation mostly evidenced by a well-marked en-chevron pattern of the scales and the appearance of an anterior nodal point (i.e., point of inversion from the anteriorly to the posteriorly directed chevrons, next to the posterior end of the interclavicle). In *Tulerpeton*, the presence of an en-chevron arrangement of the ventral scales cannot be confirmed but was most probably present since it represents the plesiomorphic condition of the ventral squamation of "osteolepiformes" (JARVIK, 1948, 1980), and is widespread in Carboniferous tetrapods (GODFREY, 1989; HOLMES 1984; HOLMES *et al*., 1998; WITZMANN, 2007). Along with the en-chevron arrangement, a median row of dorsal and ventral scales is also primitive for tetrapodomorphs (*pers. obs*.). Dorsal and ventral median rows of scales are present in *Panderichthys* (WITZMANN, 2011), but absent in *Glyptopomus* (JARVIK, 1950), and Carboniferous and Permian tetrapods (COLBERT, 1955). The condition of *Tiktaalik* and *Ichthyostega* is unknown, but in *Acanthostega*, COATES (1996) reconstructed the ventral squamation as lacking a median ventral row.

As WITZMANN (2011) proposed, the nodal-point of the ventral squamation is related to the sideward movement of the head and pectoral girdle enabling a greater degree of freedom of the forelimbs and would thus be connected to the evolution of the fore and hind limbs and their greater importance as support and locomotor structures on land. The nodal-point is characteristic of terrestrial or semi-terrestrial Carboniferous tetrapods that rely on their limbs for locomotion and show a lateral orientation of the

pectoral limbs, whereas Devonian tetrapods (such as *Acanthostega* and *Ichthyostega*) have posteriorly orientated limbs with limited degree of freedom and would have certainly rely on tail movements for aquatic locomotion (COATES, 1996; AHLBERG *et al.*, 2005; PIERCE *et al.*, 2012). Thus despite a probable en-chevron arrangement of the ventral scales in early tetrapods, including *Tulerpeton*, the presence of a nodal point as inferred by WITZMANN (2011) cannot be confirmed in *Tulerpeton*, nor in other Devonian tetrapods so far.

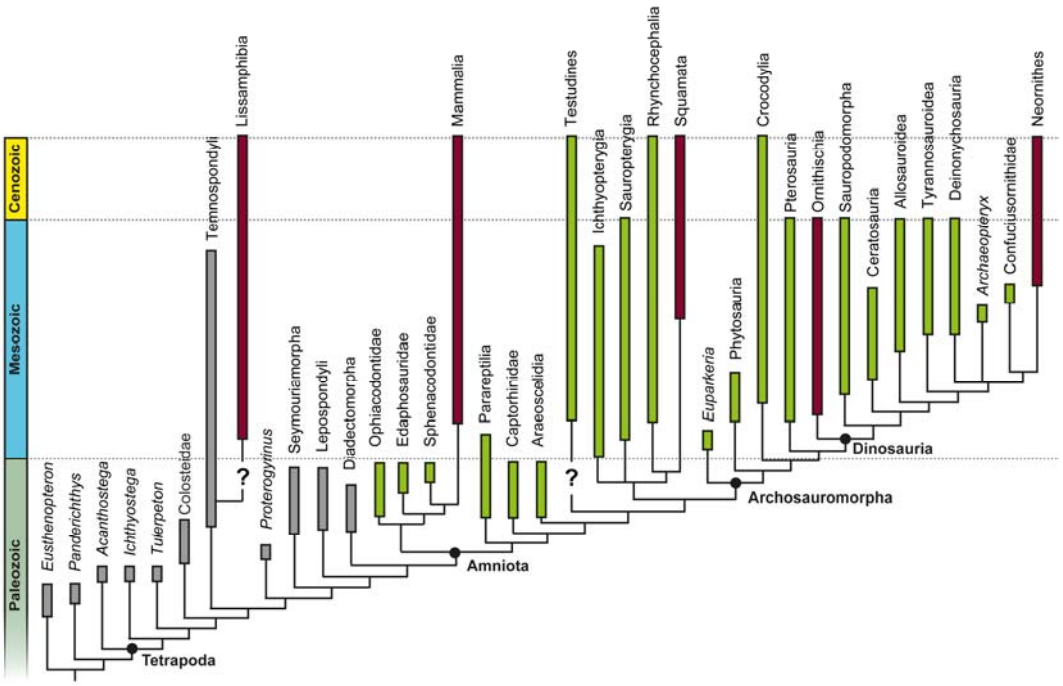



**FIGURE IV.1. Distribution of gastralia in tetrapods.** Primitive ventral (gastral) scales are present in tetrapodomorph fishes and early tetrapods (in grey). Proper gastralia (i.e., elongate rods of abdominal dermal bones arranged in chevrons) are primitively present in amniotes (in green). Loss of gastralia is convergent in lissamphibians, mammals (therapsids), lizards, snakes, ornithischian dinosaurs and modern birds (in red). Interrelationships of early tetrapods completed and modified after RUTA *et al.,* 2003; CLAESSENS, 2004.

This survey of the evolution of squamation in tetrapods led me to consider the origin of the gastralia. The gastralia, or abdominal gastral ribs, lie posterior to the sternum as a separately derived set of skeletal elements (KARDONG, 2004). Unlike the ribs that are formed endochondrally, the gastralia are of dermal origin, i.e., they mineralize without going through a cartilage-precursor phase. Gastralia may serve as an accessory skeletal system that provides a ventral surface for muscle attachment and support for the abdomen. In turtles, gastralia contribute to the building of the plastron along with other dermal elements from the ventral region (GILBERT *et al*., 2007). Gastralia are present in several amniotes (e.g., early reptiles, non-mammalian synapsids, crocodiles, dinosaurs, *Sphenodon*); they are absent from extant birds and mammals (CLAESSENS, 2004) (Fig. IV.1).

The origin of the amniote gastralia is still unclear. The current, and most commonly accepted hypothesis on gastralia evolution states that dermal ventral (gastral) scales of early tetrapods and their tetrapodomorph fish relatives preceded the gastralia functionally and perhaps gave rise to them anatomically. Like gastralia proper, the ventral scales of early tetrapods helped to support the viscera during land excursions, among other possible functions (WITZMANN, 2011), and were organized into tight, chevron-shaped rows (WITZMANN, 2007). However, it is unclear whether amniote gastralia derive from a single, and extremely elongate, gastral scale, or from the fusion of several scales from the same chevron, as seen in Carboniferous tetrapods (WITZMANN, 2011). Histological data on gastralia are extremely rare (VICKARYOUS & HALL, 2008) and the study of their origin has never been totally undertaken. New histological cross sections on Carboniferous amphibians and stem amniotes might furnish new data on the transition from gastral scales to gastralia, and possibly would allow identifying the occurrence of intermediate stages in gastralia evolution.

# V. ON THE HOMOLOGY BETWEEN SCALES AND LEPIDOTRICHIA

The question of the supposed homology between dermal scales and lepidotrichia has been a recurrent topic in every study on the histology and development of each of these structures. The assumption that scales and lepidotrichia are homologous, and more particularly that lepidotrichial segments are modified scales, was first proposed by BAUDELOT (1873) and further developed by GOODRICH (1904, 1906, 1907) and JARVIK (1959). However, this excessively straightforward scenario has been greatly criticized in recent years (e.g., SCHAEFFER, 1977; PATTERSON, 1977; GÉRAUDIE & LANDIS, 1982). I will give here a broad introduction to the problem and furnish new observations that refute the 'direct' evolution of lepidotrichia from scales. My observations agree with the consensual scenario proposed by SCHAEFFER (1977) that considers scales and lepidotrichia as belonging to a common 'morphogenetic system' and thus would share a deep homology reflected in certain similarities of their development.

As previously stated, the 'classic' works of BAUDELOT (1873b), GOODRICH (1904, 1906), and JARVIK (1959) suggested that lepidotrichia represent modified scales in all species of osteichthyans. This hypothesis was supposed to be confirmed based on morphologic studies of the dermal skeleton from the "osteolepiform" *Gyroptychius* and several "paleonisciform" actinopterygians in which 'gradual modification' in the shape of the scales towards the lepidotrichial segments at the base of the fins was observed by GOODRICH (1904). Since these fin scales were progressively transformed into plates resembling lepidotrichial segments, the changes observed were interpreted to support the view that lepidotrichia evolved *directly* from scales. However, despite a superficial similarity seen in basal forms, in advanced actinopterygians (e.g., teleosts) and extant

sarcopterygians (i.e., actinistians and dipnoans) the body scales are so different from the fin rays that we can hardly confuse them.

Scales, fin rays, scutes, and osteoderms are all manifestations of the dermal skeleton. Their belonging to the dermoskeletal system and their similar development as dermal ossifications has certainly played a role in the consideration of their supposed homology. Nevertheless, as ZYLBERBERG and WAKE (1990) cautioned, the inherent properties of the integument enable that different dermal structures such as scales and osteoderms evolve *de novo* in several taxa without need of direct descendance (e.g., the dermal scales of gymnophionans). As seen before, osseous fin rays (lepidotrichia and camptotrichia) are also mineralized products of the integument. However, osteoderms and scales, despite being integumentary mineralized products, are not considered homologous since they differ in location, structure and histology (CASTANET *et al.*, 2003). Therefore the assumed homology, or even direct descendance of the lepidotrichia from scales would not be justified based solely on the fact that both structures have a dermal origin.

The development of scales and lepidotrichia has been addressed numerous times in this thesis. Developmental data on numerous extant taxa (e.g., *Danio*, *Polypterus*, *Neoceratodus*, etc.) have shown that scales arise independently from each other whereas lepidotrichia segments form successively in a proximodistal direction (e.g., BARTSCH *et al.*, 1997; SIRE & AKIMENKO, 2004; JOHANSON *et al.*, 2009; Paper IV). In teleosts (e.g., *Danio*), scales, unlike lepidotrichia, are located at some distance from the epidermal-dermal interface with no apparent morphological relationship between the two in the early stages of development (CREASER, 1926). Only later do scales contact the basal lamina of the epidermis but this topographic location is not a primary developmental feature.

The microstructure of scales and lepidotrichia is also dissimilar. Both cosmoid and elasmoid scales show a variably mineralized basal layer (isopedine). Above the isopedine, cosmoid scales show a middle vascularised layer (spongiosa), whereas the ornamented superficial layer (external layer) of the elasmoid scales can be vascularised or not. An isopedine layer (i.e., a layer of lamellar bone with a plywood-like structure of the collagen fibres) has not been observed in any osteichthyan lepidotrichium, either in the literature or after my personal observations. The bony tissue of the lepidotrichia would thus be homologous to the scale superficial layer (spongiosa or external layer) formed by parallel-fibered bone (JARVIK, 1952; ZYLBERBERG *et al*., 2010). Moreover, in cases where the isopedine layer is present in the scales (e.g., in cosmine-covered sarcopterygians, extant coelacanths and dipnoans, lepisosteid actinopterygians, etc.), the lepidotrichia never show a basal bony layer. The only addition to the uniform lamellar-bone forming the rays are the odontogenic contributions (i.e., cosmine, odontodes, ganoine), located in the outer portion of the lepidotrichia.

The similarity between scales and fin rays is thus only superficial due to the covering of cosmine. In cosmine-covered sarcopterygians, the similarity between the fin scales and the lepidotrichial segments can be astonishing and the transition from scales to fin rays is sometimes difficult to observe. For instance, JARVIK (1959) considered that in *Porolepis* the fin rays and the scales were part of the same anatomical complex in which the large basal scales of the lobate fins gradually diminished their size distally to become more or less elongate rectangular plates (i.e., segmented lepidotrichia) forming the fin rays. Moreover both structures, scales and fin rays, are covered externally by a layer of cosmine thus blurring the morphological gap between scales and rays. However, due to the characteristics of fossil preservation it was not possible to determine whether the proximal, and possibly unsegmented, lepidotrichia pass under the squamation and

articulate with the endoskeletal radials of the fin (CLÉMENT, 2004) or if they lie in close contact with the basal fin scales as suggested by JARVIK (1959) and discussed by CAMPBELL & BARWICK (1988) about *Uranolophus*. A study currently in progress with co-authors using new data obtained by X-rays synchrotron microtomography on *Porolepis* fin material from Spitsbergen would shed more light on this issue (Fig. V.1). But I can say that most certainly the lepidotrichia will show a long unsegmented proximal region articulating with the radials, similar to the condition of holoptychiids, and that such unsegmented portion would be devoid of cosmine as in other cosmine-covered sarcopterygians.

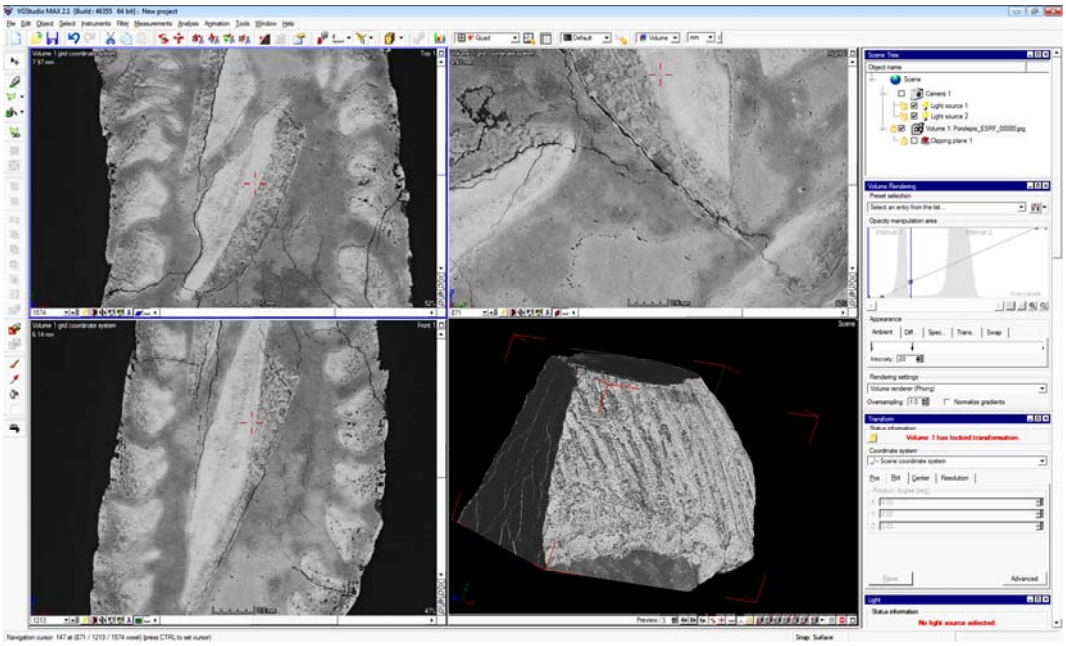


**FIGURE V.1. VG Studio Max ® interface during the initial treatment of the fin base fragment of *Porolepis* (MNHN.f. SVD 4319 A/B) based on images obtained by synchrotron light.** See Chap. II, Fig. II.2.3.1. for comparisons with Mimics ® interface.

The presence of cosmine and of other odontogenic products such as ganoine, in the superficial exposed portion of the lepidotrichia evidences the importance of

epidermal-dermal interactions during the formation of integumentary structures. As previously seen, enamel is deposited by ameloblast, housed in the epidermis. As stated in the Introduction, the position of the scale in the dermis changes during growth; the posterior margin, and eventually the exposed area pushes against the epidermis, while the anterior end sinks into the deeper layers of the dermis and becomes overlapped by the anterior scale row (CREASER, 1926). Curiously, enamel (in cosmoid or ganoid scales) is only present in the exposed area of the scales and fin rays (*pers. obs.*), thus in the portion of the scales and rays directly contacting the epidermis*;* the overlapped area of the scales and the deeply buried proximal unjointed portion of the lepidotrichia, which is always covered by scales, do not show cosmine or ganoine. This 'restricted' occurrence of enamel evidences the importance of epidermal contact in the deposition of the enamel. However, it does not imply that structures showing enamel (i.e., scales and lepidotrichia) are directly homologous, but rather that the 'spatial' constraints of their development (i.e., the contact between the superficial, exposed areas with the epidermis) are similar, resulting in a similar enamel covering.

Developmental data on the zebrafish have shown that in *Danio* scales begin forming 30 days post-fertilization (SIRE & AKIMENKO, 2004). Lepidotrichia are already formed and ossified by then (KIMMEL *et al*., 1995, BIRD & MABEE, 2003). If we consider that scale formation always occurs after lepidotrichia formation in all osteichthyans (as evidenced in *Neoceratodus*, KEMP, 1981 and *Polypterus*, BARTSCH *et al*., 1997), then every tissue common to scales and lepidotrichia has to be added to the lepidotrichia *after* the formation of both scales and lepidotrichia. Moreover, as ØRVIG (1969a) showed, scale cosmine occurs only in juvenile to adult stages, thus way after the ossification of the lepidotrichia.

To sum up, I consider that the similarity between scales and lepidotrichia is only superficial due to the covering of cosmine that blurs the separation between body scales and fin rays. On the basis of embryologic and structural features, it may seem inappropriate to apply to the bony tissue forming the lepidotrichia the hypothesis that the segments of fin rays are modified scales in all osteichthyans (HALL, 2005). However, scales are considered to be neural crest–derived (DONOGHUE *et al*., 2008) and it has been recently shown that neural crest cells derivates contribute to lepidotrichia formation (SMITH *et al*., 1994). Thus, it is perhaps more meaningful to consider that "scales and lepidotrichia composed of enamel, dentine and bone are somewhat different morphological manifestations of the same morphogenetic system", as proposed by SCHAEFFER (1977:44). This would imply that scales and lepidotrichia share a deep homology of their developmental features, but their similarities do not imply that the former gave rise to the latter.

**THE FULCRA –** The case of the actinopterygian fulcra complicates the supposedly 'straight' distinction between scales and lepidotrichia. The fulcra are osseous, scale-like, elements located at the margin of the paired and/or unpaired fins of most actinopterygians (e.g., JARVIK, 1959; GARDINER, 1984; ARRATIA, 2008, 2009). Absence of fulcra is characteristic of sarcopterygian, although 'fulcral' scales have been identified in *Psarolepis* (QU, *pers. comm*., 2012). Fulcra can be unpaired and paired elements depending on the actinopterygian group (see ARRATIA, 2008, 2009). Usually, when both paired and unpaired fulcra occur in a certain taxon, the more anterior basal fulcra are unpaired with forked proximal bases and the most posterior fulcra are paired. Moreover, basal fulcra appear to be always covered with a layer of ganoine in many fossil and basal actinopterygians (e.g., the extant *Lepisosteus*) (GOODRICH, 1904). A thin

layer of ganoine or remnants of ganoine are found in fossil basal teleosts bearing fulcra (ARRATIA, 2008). Along with basal fulcra, actinopterygians can also show fringing fulcra, which are defined as paired structures associated with the leading rays of paired and/or unpaired fins (ARRATIA, 2008).

These examples in actinopterygians illustrate the plasticity of the fin scales and lepidotrichia. For instance, ARRATIA (2008, 2009) stated that the so-called procurrent rays (or rudimentary rays *sensu* GRANDE & BEMIS, 1998) of unpaired fins found in derived actinopterygians are the result of the progressive developmental and evolutionary transformation of the basal fulcra. Similarly, fringing fulcra are clear derivatives from lepidotrichial segments. Therefore, we could say that basal fulcra evolved into 'lepidotrichial segment-like' elements in certain derived actinopterygians, and therefore that the so-called procurrent rays could be considered homologous to the basal fulcra. A segmented procurrent ray would thus be formed by several modified fulcra, similar to the segments of a 'normal' lepidotrichium. Nevertheless, these structures (basal fulcra, fringing fulcra, and procurrent or rudimentary rays) are 'external additions' to the fin web and play a morphofunctional role in the establishment of a continuum between the body walls and the fin web. Moreover, ARRATIA (2008, 2009) clearly established the differences in the caudal fin between principal rays (forming the main part of the web) and the 'marginal' rays (e.g., procurrent rays), usually unsegmented and discontinuous with the principal rays.

The fulcral scales and/or lepidotrichial segments do not contradict the point formerly stated of a different origin, but similar development, of scales and lepidotrichia. The superficial similarities between both structures might merely be linked to their morphofunctional importance in the leading margins of fins and to the common, and limited number of, components and modes of development of dermoskeletal structures.

## VI. CAUDAL FIN EVOLUTION IN SARCOPTERYGIANS

Throughout his career, AGASSIZ established a theoretical framework, the so-called the 'three-fold parallelism', that combined for the first time data obtained from "embryonic growth" (i.e., embryology), "structural gradation" (i.e., phylogeny), and "geological succession" (i.e., palaeontology). To AGASSIZ, the order of appearance of animals in the fossil record largely mirrored the order of appearance of their morphological features during development, and that in turn mirrored their phylogenetic relationships. One of the most famous examples of this 'three-fold parallelism', at least for ichthyologists, is the ontogenetic and paleontological sequence of caudal fin development and evolution in bony fishes.

In actinopterygian teleosts, the embryos show a protocercal caudal fin that first become heterocercal in the larvae and, finally homocercal in the adult. AGASSIZ considered that this ontogenetic sequence mirrored the appearance of this caudal fin morphotypes in the fossil record, with the basal osteichthyans like lungfishes showing homocercal (or diphycercal) tails, basal actinopterygians like sturgeons showing heterocercal tail, and derived actinopterygians (i.e., teleosts) showing homocercal caudal fins. Thus, the teleosts tail ontogeny of appears to recapitulate its phylogeny in a very 'haeckelian' way (AGASSIZ, 1878).

The caudal fin evolution in osteichthyans has puzzled anatomists and palaeontologist since the origins of ichthyology (e.g., VON BAER, 1853; HUXLEY, 1859). Relationships between developmental biology and palaeontology in studies of the tail of teleosts were reviewed by METSCHER and AHLBERG (2001). Most of these studies have focused in actinopterygians, surely because of the larger amount of data and experimental possibilities with living model organisms (e.g., zebrafish, medaka). In

actinopterygians, the transition from a primitive heterocercal to a derived homocercal tail in teleosts is now relatively well known, both developmentally (BEMIS & GRANDE, 1999) and paleontological (METSCHER & AHLBERG, 2001). However, the transition from heterocercal to diphycercal tail (and viceversa) in sarcopterygians is a lesser-explored issue. In order to introduce certain elements of discussion to this topic, it is essential to return to AGASSIZ's 'three-fold parallelism' and combine data from embryology, phylogeny, and fossil morphologies.

The earliest vertebrates, both extant and extinct, show a hypocercal caudal fin in which the posterior tip of the notochord points ventrally (JANVIER, 1996; PRADEL *et al.*, 2007). A hypocercal tail thus seems to be the general condition for vertebrates and was subsequently modified into a variety of caudal fin morphotypes. Heterostracans and furcacaudiform "agnathans" show hypocercal but superficially symmetrical tails. Osteostracan "agnathans" are the first vertebrates with epicercal caudal fins, in which the posterior tip of the notochord no longer points ventrally, but dorsally. This condition was maintained in gnathostomes (e.g., placoderms, chondrichthyans, and osteichthyans).

Although it is clear that the heterocercal condition is primitive for gnathostomes, and certainly evolved from the condition of osteostracans, it remains unclear whether the heterocercal tail is also the primitive condition for osteichthyans. By comparison with out-groups, such as "acanthodians" and chondrichthyans, it appears to be so. Nevertheless, the acceptance of a primitive heterocercal tail for osteichthyans has been widely taken for granted, simply because of its prevalence as an easily recognizable external feature. However, when we consider the internal structure of the tail and its development, it gets more complicated. In all cases of heterocercal tails, the distal epichordal radial series is absent or unossified. As LUND and LUND (1985) pointed out in

their survey of Carboniferous coelacanths, it is very unlikely to expect that distal radials would fully reappear *de novo* in the transition from a heterocercal to a secondarily diphycercal tail, all the more that such transition is known to have occurred several times in sarcopterygians (Fig. VI.1). Chondrichthyans, reputedly known by their archetypical heterocercal caudal fins, also appear to contradict the 'classic' scenario of the primitiveness of the heterocercal condition since certain Palaeozoic forms show internally symmetrical tails (JANVIER, 1996). However, the discovery of challenging new fossils and recent promising developmental data are showing that it might be possible that disparate set of tail morphotypes of osteichthyans could derive from a primitive symmetrical 'diphycercal-like' caudal fin instead of the 'classical' heterocercal tail.

The first evidence came from palaeontology. PRADEL *et al.* (2007) studied the caudal fin of *Sacabambaspis janvieri*, an arandaspid "agnathan" from the Ordovician of Bolivia. *Sacabambaspis* shows a hypocercal caudal fin, but the authors contemplated the possibility that the tail of *Sacabambaspis* may have been isocercal, with almost equal-sized caudal lobes extending dorsal and ventral to the notochord. This isocercal condition is similar to the diphycercal tail of certain fossil chondrichthyans, onychodontids, and 'anatomically modern' actinistians (ZHU *et al.*, 2012a). PRADEL *et al.* (2007) even regarded the isocercal condition as primitive for vertebrates, as it vaguely resembles the isocercal tail of cephalochordates, whose median fins are nevertheless not supported by cartilaginous radials (CHEN, 2008).

Concerning the transition from hypocercy to epicercy in early vertebrates, it is plausible to consider that a genetic 'switch' in the developing tail is responsible for the inversion of the dorso-ventral polarity in the caudal fin during vertebrate evolution. Genetic mutations or chemical knockdowns may show phenotypes of polarity inversion of caudal structures and embryonic caudal 'ventralization' or 'dorsalization' (e.g. HAFTER

*et al.*, 1996; PAYNE *et al.*, 2001; LITTLE & MULLINS, 2004). Through this $180^0$ switch, the ventral lobe would become dorsal, and viceversa, and the posterior tip of the notochord would turn out pointing dorsally. This scenario would be consistent with the occurrence of well-developed dorsal lobes in all hypocercal "agnathans", and the 'sudden' transition to epicercy with well-developed ventral lobes in osteostracans and gnathostomes.

Focusing on gnathostomes, SCHULTZE and CUMBAA (2001) described the postcranial anatomy of the osteichthyan *Dialipina salgueiroensis* from the Early Devonian of the Canadian Arctic. Based on several articulated specimens, *Dialipina* was then reconstructed as one of the basal most actinopterygians. Two of the more striking features of *Dialipina,* when considering its attribution to the Actinopterygii, are the presence of two dorsal fins and a 'triphycercal' caudal fin with symmetrical dorsal and ventral lobes and well-developed middle lobe. The shape and the arrangement of fin rays in the 'triphycercal' tail of *Dialipina* are similar to the diphycercal tail of the onychodontid *Strunius*. The recent revision of osteichthyan interrelationships by FRIEDMAN and BRAZEAU (2010) considers *Dialipina* as a stem osteichthyan, not belonging to the actinopterygian crown group. If this position is confirmed it would imply that diphycercal (i.e., triphycercal) caudal fins are primitive for osteichthyans, and that early sarcopterygians, such as onychodontids, show diphycercal fins as a retention of this primitive character. The same is true for the occurrence of two dorsal fins, a feature retained in sarcopterygians, but reduced to a single dorsal fin in actinopterygians.

SCHULTZE and CUMBAA (2001) considered that the diphycercal caudal fins of sarcopterygians and actinopterygians were acquired independently. This is probably true in sarcopterygians for groups in which the earliest representatives show heterocercal tails and later evolved diphycercal caudal fins (e.g., actinistians, dipnoans, rhizodontids, tristichopterids) (Fig. VI.1). However, the primitive condition is more

difficult to interpret in terms of convergence. The caudal fin of stem sarcopterygians is unknown (e.g., *Guiyu*, *Psarolepis*), but ZHU *et al.* (2009, 2012b) parsimoniously reconstructed *Guiyu* with a diphycercal caudal fin shape (see Chap. I, Fig. III.3.1.1) similar to that of *Dialipina* and *Strunius*. However, the current phylogenetic scenario of osteichthyan interrelationships does not furnish more clues about the evolutionary sequence of events involved in the transition from one tail morphotype to the other. It seems that currently we have reached a phylogenetic impasse and that no elegant solution can be found in the fossil record.

New data on the genetic and developmental basis of caudal fin evolution have shed more light on this issue. MORIYAMA *et al.* (2012) investigated in the medaka (*Oryzias latipes*) the genetic differences between wild type fishes and the spontaneous mutant *Double anal fin* (*Da*) that exhibits a diphycercal caudal fin, as opposed to the classic homocercal tail of other teleosts. The authors evidenced the occurrence of a sclerotome rich mesenchyme in the tail region of medaka and zebrafish, from which hypurals and epurals will later develop forming the endoskeletal portion of the caudal fin. They called this region CSM ('caudal skeleton forming mesenchyme'). The authors showed that in wild type fishes, the CSM was more developed ventrally, and thus adults showed a more developed ventral lobe that will result in the formation of the homocercal tail characteristic of teleosts. In *Da* mutants, the CSM occupied a larger area, both ventral and dorsal to the notochord, resulting in a diphycercal tail through the symmetrical development of the endoskeleton in both sides of the notochord. Moreover, in the *Da* mutant, the dorsal and anal fins are almost identical, both in shape and position in the posterior half of the body, as a result of the anterior expansion of the dorsal fin.

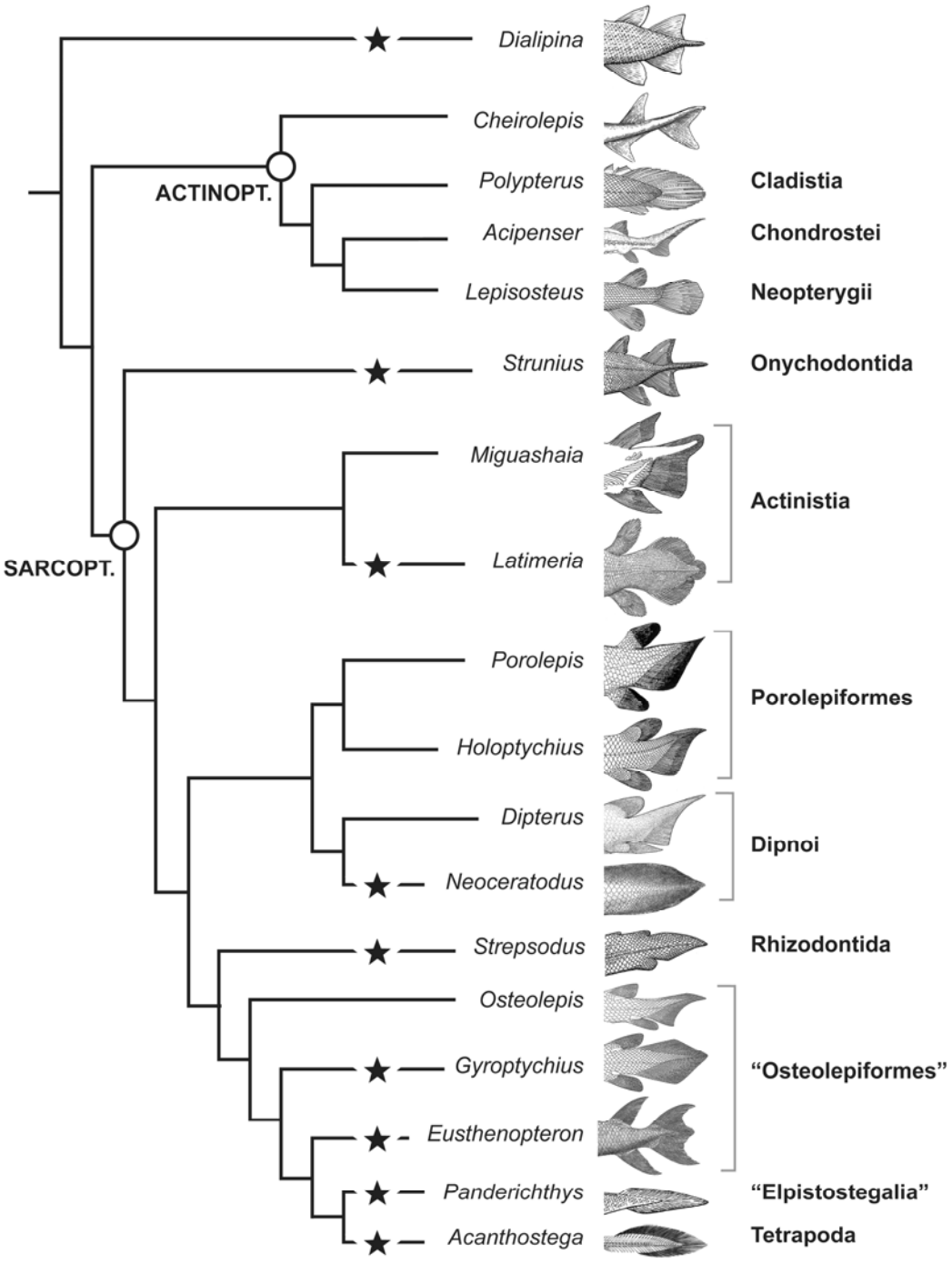



**FIGURE VI.1. Caudal fin evolution in osteichthyans with especial reference to the distribution of diphycercal tail.** The primitive condition of osteichthyans is probably a diphycercal tail as present in the stem osteicththyan *Dialipina* and onychodontids. However, heterocercal tail appear very early in crown osteichthyans. Posterior evolution of a diphycercal caudal fin from a heterocercal condition is probably a convergent event in sarcopterygians. Diphycercal tails are represented by a star. Drawings after JARVIK, 1980; AHLBERG & TREWIN, 1995; COATES, 1996; CLOUTIER, 1996; JANVIER, 1996, 2007; CLÉMENT, 2004.

The authors also showed that expression of *zic1*/*zic4* genes is related to the dorsal bending of the notochord and to the asymmetric development of the caudal fin skeleton, not only in medaka but also in the zebrafish, thus suggesting that the developmental system of an asymmetric caudal fin is maintained in teleosts. However, in the *Da* mutant the bending of the notochord does not occur. Moreover, the *twist* gene, responsible for the differentiation of sclerotome-derived cells into osteoblast during development of the vertebra in medaka, is overexpressed dorsal to notochord leading to a symmetrical development of epurals and hypurals.

This study has a great explanatory potential to our understanding of the caudal fin evolution in osteichthyans and the puzzling occurrence of a diphycercal tail in numerous lineages of sarcopterygians. Indeed, MORIYAMA *et al.* (2012) proposed that downregulation of *twist* in the CSM dorsal to the notochord would lead to hypoplasia of the epurals, and thus contribute to accentuate the differences between dorsal and ventral lobes in the homocercal teleost tail. Therefore, it implies that CSM has the potential of forming caudal endoskeletal elements in both sides of the notochord, but that this totipotency is 'tuned' by regulatory molecules. The CSM has proven to be a common feature of teleosts, but it is also highly probable that similar 'caudal skeleton forming mesenchyme' is present in more basal actinopterygians, and even in osteichthyans as a whole.

Since the acquisition of a homocercal tail in teleosts is likely due to fine regulation of the potential of the CSM to form caudal fin radials (MORIYAMA *et al.*, 2012), along with a probable homeotic duplication of the ancestral ventral lobe (METSCHER & AHLBERG, 2001), it could be stated that a symmetrical diphycercal caudal fin, similar to that of the *Da* mutant in medaka, was present in the earliest osteichthyans. Subsequent evolution of a heterocercal caudal fin would thus be the result of slight modifications of

the CSM potential to form symmetrical tails and produce a dorsal bending of the notochord. Moreover, the 'return' to a diphycercal condition in lineages where ancestral representatives show heterocercal tails (e.g., actinistians and numerous tetrapodomorphs), could thus represent a regain of the ancestral condition through downregulation of the molecules responsible for the asymmetrical development of ventral and dorsal lobes. Further studies should thus try to identify the presence of CSM in other osteicthyans and study the genetic and developmental mechanisms responsible for divergent development of the dorsal and ventral portions of the tail.

## VII. THE LOSS OF FIN RAYS IN TETRAPODS

The absence of fin rays is an important feature of tetrapods. The loss of lepidotrichia in the paired fins in tetrapods is strongly related with the modifications of the appendicular skeleton during the fish-tetrapod transition and the origin of digits. However it may be too straightforward to assert that the evolution of digits and 'digit-like' structures in the paired fins of tetrapodomorphs is linked to the loss of the lepidotrichia (AHN & HO, 2008). For instance, rhizodontids still retain long lepidotrichia in their 'limb-like' paired fins (DAESCHLER & SHUBIN, 1998). Morphological plasticity of the endo- and dermoskeleton in the paired and medians fins of tetrapodomorph fishes suggest a developmental link between both structures that was, somehow, broken in tetrapods. In this sense, the loss of the lepidotrichia in both the paired and the caudal fins took place independently, and therefore the underlying developmental mechanisms could only be applied locally. The explanation of either one of these losses might not strictly apply to the other.

The retention of a 'fish-like' caudal fin is certainly the most noticeable primitive trait of Devonian tetrapods. As evidenced by LUND and LUND (1984) in actinistians, the shape of the caudal fin in sarcopterygians, whether rounded, elliptical, or squared, is a highly adaptive character related to acceleration, aspect ratio, and drag. The presence of a well-developed tail supported by fin rays in early tetrapods (as present in *Acanthostega* and *Ichthyostega*, and probably also occurring in other Devonian tetrapods) is thus a strong marker of their aquatic way of life, their swimming style, and their close relationship with piscine sarcopterygians.

The presence of a well-developed caudal fin with lepidotrichia in Devonian tetrapods, and more importantly, in the most completely known tetrapod *Acanthostega,*

is thus a strong evidence to support that tetrapods evolved in water from aquatic ancestors from the "elpistostegalian" stock. There is little anatomical and/or developmental evidence that fin radials and lepidotrichia might have disappeared during an earlier transition to land and then regained in a secondary aquatic adaptation for tetrapods such as *Acanthostega* and *Ichthyostega* (CLACK & COATES, 1995).

As seen in the introduction, Devonian tetrapods might have swum by powerful lateral sweeps of their tails, as modern crocodiles do. The loss of other median fins and the presence of digits in the paddle-like paired fins left the caudal fin as the main source of thrust. Tetrapod's caudal fins were stiffer than those of other sarcopterygians. The unsegmented lepidotrichia, with a rather long proximal section articulating with the fin radials, would have prevented flexible, 'fan-like' movements of the tail as seen in the large median fins of actinopterygians (DRUCKER & LAUDER, 2002; LAUDER & DRUCKER, 2004). Instead, fin rays might have followed the lateral flexion of the vertebral column, with little perpendicular deviation of the rays. The main thrust production would thus rely on the tail as a whole and not on the fin web as in other fishes.

The shape of the caudal fin is also indicative of the degree of 'terrestrialization' of these forms and the approximate time amount spent on land. The absence of lepidotrichia and the modifications of the radials in the anterior part of the ventral lobe of the tail fin in *Ichthyostega* show that the tail certainly rested or dragged on the ground when the animal was on land or in shallow waters. A similar scenario can be proposed for *Acanthostega* and even for "elpistostegalians". Logically, the ventral region of the body would have been in contact with the ground or the substrate more often than the dorsal one. Therefore, the posterior displacement of the lepidotrichia of the ventral lobe would have enabled the animals to rest on their bellies more easily and/or more often. This posterior displacement of the fin rays would have thus prevented the caudal fin

from injury during land incursions. It is logical to suppose that lepidotrichia were reduced and even disappeared in this region of the tail, and eventually throughout the caudal fin, in connection with the transition from water to land during the Late Devonian.

Lepidotrichia are considered to have completely disappeared from tetrapods after the Devonian. However, recently, CLACK (2011) described the presence of long, unsegmented lepidotrichia next to a partial caudal portion of the vertebral column of a Late Carboniferous embolemere tetrapod. CLACK proposed that such lepidotrichia could belong to the embolomere due to the presence of supraneural radials, a common condition in the tails of fishes (MABEE, 1988) and Devonian tetrapods (COATES, 1996; JARVIK, 1996). However, lepidotrichia were not found in articulation with the tail skeleton, and thus she also considered that since the lepidotrichia could not be definitely attributed to the embolomere, they could belong to a large sarcopterygian fish, such as a dipnoan. However, by that time, the lepidotrichia of dipnoans showed the 'classical' segmented and distally branched osteichthyan condition, although with a rather long unsegmented proximal region (Paper IV). Due to their size, such long unjointed lepidotrichia would have probably belonged to the embolomere itself, and therefore would confirm the relationship between the maintenance of dermal lepidotrichia and endoskeletal radials in post-Devonian tetrapods. Another possibility is that these lepidotrichia might belong to a rhizodontid, which are known to posses long unsegmented lepidotrichia in the paired and median fins by the Late Carboniferous and were also dwelling in fresh waters.

The loss of lepidotrichia in tetrapods is a distinctive feature of the fish-tetrapod transition. This morphological change involves the reduction in thickness and loss of the odontogenic component of the scales (Paper III), the reduction of median fins in

"elpistostegalians" and tetrapods, and the loss the fin rays in post Devonian tetrapods. These examples attest of the progressive reduction of the dermal skeleton in vertebrates during the Middle to Late Palaeozoic, representing an economy in elements and structure (JARVIK, 1980). The modification and 'sudden' disappearance of the lepidotrichia in post Devonian forms, and the changes observed in the morphology and pattern of the dermal scales between Devonian and Carboniferous tetrapods (Paper III), has led to the proposition of a series of hypotheses to account for the diminishing importance of the dermal skeleton in the trunk and fins during the fish-tetrapod transition.

Here I will review and discuss the main hypotheses dealing with the loss of fin rays in tetrapods. I will also propose a novel hypothesis based on my personal observations and the preliminary results of the developmental biology experiments and discussions with my supervisors. This part should have been integrated in the discussion of Paper IV, but due to the preliminary state of the manuscript, I decided to include it here in a more extended version.

SMITH *et al.* (1994) demonstrated a contribution of neural crest-derived mesenchyme to the formation of caudal fin lepidotrichia in the zebrafish. The continuous median fin of larval amphibians contains mesenchyme of neural crest origin (EISEN & WESTON, 1993) but the fin is not supported by fin rays of any kind. Based on the work of SMITH *et al.* (1994), HALL (2005) was among the first to propose that since lepidotrichia are considered neural crest derivatives in actinopterygian and sarcopterygian fins, their disappearance in tetrapods might have been correlated with a loss of the ability of neural crest cells to undergo skeletogenesis in the paired and median appendages. Indeed, neural crest cells do not generally contribute to bone formation in the trunk region in extant tetrapods, but there are exceptions, such as in

some shoulder girdle bones (MATSUOKA *et al*., 2005), the gastral ribs (gastralia) of certain amniotes (VICKARYOUS & HALL, 2008), and the plastron of turtles (CEBRA-THOMAS *et al*., 2007). Recently, marker genes for neural crest cells have been identified in chondrichthyan median fins (FREITAS *et al*., 2006) and MCGONNELL and GRAHAM (2002) demonstrated the skeletogenic potential of trunk neural crest in the chick. Further studies are needed in order to better understand the contribution of neural crest cells to the appendages of tetrapods and the stretch of their skeletogentic potential.

A recent study has drawn the attention on the evolutionary loss of lepidotrichia in tetrapods. ZHANG *et al*. (2010) proposed a new hypothesis for the loss of fin rays and the modification of paired appendages during the fish to tetrapod transition. The authors examined the relationship between the loss of fin rays and the genomic loss of the Actinodin (*And*) family genes. These genes are involved in the construction of the collagenous actinotrichia, functional precursors of the lepidotrichia. The knockdown of *And* genes causes the loss of actinotrichia, followed by failure in the migration of mesenchymal cells that will form the lepidotrichia using the actinotrichia as a scaffold. Moreover, DURÁN *et al*. (2011) showed that the downregulation of *col2a1b* production by morpholino injection also lead to absence of actinotrichia and fin fold mesenchyme during zebrafish embryogenesis. Interestingly, *And* genes and the actinotrichia collagen *col2a1b* have not been found in any tetrapod species (ZHANG *et al.*, 2010; DURÁN *et al*., 2011).

ZHANG *et al*. (2010) proposed that loss of these genes associated with the collagenous component of zebrafish fins (actinotrichia) might have not only lead to a loss of the fin dermoskeleton (lepidotrichia), but also to an unusual proliferation of the endoskeletal portion of the fin. This endoskeletal proliferation might have been related to the production of extra digits characteristic of the limbs of early tetrapods such as

*Acanthostega*. The authors proposed that the loss of actinotrichia during evolution might have induced profound changes in the morphology of the adult pectoral fins. These changes perhaps led to short appendages without lepidotrichia and to gene expression profiles conducive to polydactyly in the earliest tetrapods. However, and perhaps more importantly, the results show that the effects of the loss of function of and1 and and2 in zebrafish seem to be less drastic in the tail, and lepidotrichia may develop normally. This pattern might be reminiscent of the condition of Devonian tetrapods, which retained a fin ray-supported caudal fin. Therefore, elegant as these experiments might be, it seems that loss of the *And* genes explains only partially the loss of lepidotrichia in tetrapods, ie., the absence of lepidotrichia in the paired fins. However, many more studies should be done for a concrete hypothesis to be suggested. For instance, collagen type I mutation *chihuahua* may show absence of actinotrichia without perturbing lepidotrichia formation (DURÁN *et al*., 2011). In principle, this result would rule out the simple and elegant hypothesis by ZHANG *et al.* (2010).

**A NEW HYPOTHESIS** – During my stays in the UMA, I gathered a large amount of information on fin ray structural diversity and began to identify evolutionary and developmental patterns in the fins of osteichthyans. Along with my supervisor, Manuel MARÍ-BEFFA, we established a new evolutionary model for the structural and developmental diversity of the lepidotrichia (this model called the 'Fin Ray Patterning module' will be included in Paper IV). We also proposed a scenario to account for the morphological variation of the lepidotrichia in tetrapodomorphs and their eventual loss in tetrapods. Based on observations of the fins in sarcopterygians, and particularly in tetrapodomorph fishes, we concluded that the loss of the fins rays in tetrapods could be an inherent property of fin rays that follows a general developmental trend to distalize

fin structures along the proximo-distal axis. This distalization is correlated with the fin endoskeleton proliferation and its overlap by the proximal unjointed portion of the lepidotrichia.

As seen in the Introduction and thoroughly explained in Paper IV, the basic pattern of the lepidotrichia consists of a distally bifurcated ray, a series of repetitive segments in the middle part, and an unjointed and elongate proximal portion that articulates with the radial bones of the fins. Segmentation and bifurcation are independent processes, regulated by different genes, but they are related during development (MARÍ-BEFFA & MURCIANO, 2010). Segmentation and bifurcation share common genes that act upstream during fin ray development. If the expression of these key genes is modified in a certain way, both segmentation and bifurcation are affected.

In our model, the fin is viewed as a composition of developmental and evolutionary units. Each unit may be composed by a ray and half of both neighbouring interrays (i.e., the mesenchyme lying between two lepidotrichia in living fishes). These elements need to be present for a complete morphology to be observed. The morphology of rays and inter-rays are dependent on mechanisms controlling polarity and pattern during early and late development. Three organizers regulate the general pattern in the early fin bud: 1) the apical ectodermal ridge, 2) the zone of polarizing activity, and 3) dorso-ventral interactions in the fin bud ectoderm (see MARÍ-BEFFA & MURCIANO, 2010; Paper IV).

During late development, two organizers, the distal and the ray-interray organizers, and contralateral interactions between apposed hemirays regulate the process from fin fold outgrowth to adulthood (MURCIANO *et al.*, 2001, 2007; MARÍ-BEFFA & MURCIANO, 2010). The three embryonic organizers are almost identical to those observed in the early development of the tetrapod limb (MERCADER, 2007; YANO & TAMURA, 2012).

These three organizers provide polarity and patterning along the orthogonal proximo-distal, antero-posterior and dorso-ventral axes. However, during late development, other signalling mechanisms enter the scene of the development of the fin dermoskeleton. A distal organizer, dependent on epidermis-mesenchyme interactions, controls the proximo-distal axis. The ray-interray organizer, dependent on interactions between the rays and neighboring interrays, locally controls the antero-posterior axis. Finally, contralateral interactions, also dependent on epidermis-mesenchyme interactions, regulate polarity and pattern along the dorso-ventral orthogonal axis.

The regulatory effect and morphological implications along these three axes are easily discernible in living specimens, either through *de visu* observation of fin anatomy or by cross sections (see Paper IV, fig. 8). However, when we consider fossils, interray spaces are normally absent due to the coalescence of the fin rays during diagenesis. Therefore, in fossil specimens only the proximodistal axis of the fin rays is completely informative. As suggested in references above, ray bifurcations are dependent on signals coming from the three organizing systems so that some indirect information on these other signalling could be deduced from fossil fin morphologies.

In gnathostomes crownward to chondrichthyans (i.e., Teleostomi, including certain "acanthodians" and osteichthyans, BRAZEAU, 2009), lepidotrichia substitute ceratotrichia as the main rays supporting the fins. The actinotrichia of osteichthyans, homologous to the ceratotrichia of chondrichthyans and "placoderms" (CARR *et al.*, 2010), are progressively distalized during ontogeny as formation and ossification of the lepidotrichia progresses proximo-distally (Paper IV, fig. 3). In sarcopterygians, a gradual distalization of the segmentation (and therefore, an elongation of the unjointed proximal portion) is also observed in the lepidotrichia of actinistians, dipnoans, and rhizodontids (*pers. obs.*). A distalization of the segmentation was observed in *Tiktaalik* (SHUBIN *et al.*,

2006), however such distalization is not present in *Panderichthys* (AHLBERG, *pers. comm*., 2012). Distalization of the segmentation is ubiquitous in early dipnoans (CLOUTIER, 1996b; ARRATIA *et al*., 2001), and extreme in rhizodontids (JEFFERY, 2001; JOHANSON *et al*., 2005b). In Devonian tetrapods (e.g., *Acanthostega*) the lepidotrichia are totally unjointed. Curiously, elongation of the proximal portion of the lepidotrichia related, in almost all cases, to the distal expansion of the overlapping fin scales.

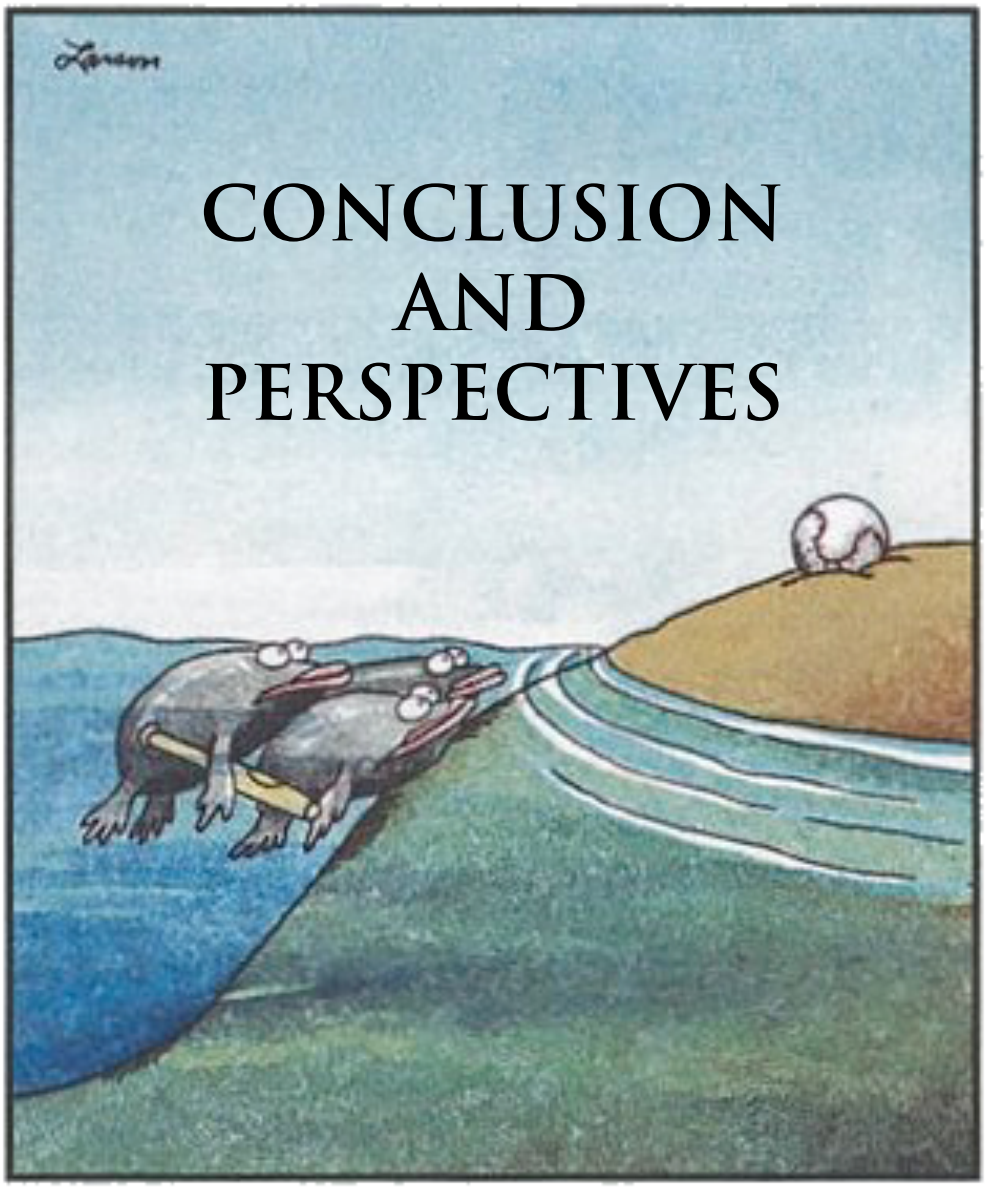
This phylogenetic series of phenotypes matches certain proximo-distal processes observed during normal development, such distal displacement of the actinotrichia by proximal resorption, fusion of lepidotrichial segments resulting in the elongation of the proximal portion of the rays, and gradual distalization of the bifurcation from the posterior to the anterior of the fins.

Conclusions from developmental and regenerative biology thus parallel phylogenetic and paleontological observations. From all these evidences, a trend emerges: fin ray features of the fins of osteichthyans show a gradual positional transformation of characters towards the distal position of the fin. This transformability feature may have its roots in the generative mechanism of normal fin development as suggested by developmental studies (reviewed in MARÍ-BEFFA & MURCIANO, 2010).

My experiments with FGFs mutants and inhibitor treatments were based on the following starting hypothesis: if the genetic pathways regulated upstream by FGF are affected due to mutations or a default in FGF expression, changes in the developmental pattern can be observed (LEE *et al*., 2005). These changes commonly affect growth rate or would lead to complete failure of the development of certain structures. However, it is also probable that slight, 'modulable' changes had morphological consequences that could be identified. In the zebrafish with dominant negative Fgfr1, both growth rate (LEE *et al*., 2005) and morphological changes (see also MARÍ-BEFFA & MURCIANO, 2010) can

occur during fin regeneration. These morphological changes are expected to be visible in the fin rays, such as suppression of distal bifurcation, distalization of joints, or inhibition of segmentation altogether, etc. By experimental modulation of the effect of the loss of FGF action during fin formation, we would be able to observe the eventual morphological changes in the lepidotrichial pattern of segmentation and bifurcation. The experiments have been performed but the expected results are not yet ready to be presented.

# CONCLUSION AND PERSPECTIVES



Great moments in evolution

# I. GENERAL CONCLUSIONS

The scales and fin rays of sarcopterygian fishes have proven to be very informative structures in the study of the evolutionary modifications that have occurred during the fish-tetrapod transition in the Devonian. The combination of paleontological and developmental data has provided several encouraging results and emphasized the importance of pluridisciplinary studies in the field of early tetrapod evolution. Here I shall briefly present the main conclusions of my research, first for the scales and second for the fin rays.

**THE SCALES** – The evolution of the squamation in osteichthyans seems to occur on two levels, matching the two main portions of the scales (i.e., superficial and basal). These two portions show independent evolutionary trends, thus suggesting separate developmental origins. Indeed, loss of tissues (e.g., cosmine, isopedine) can occur in one portion of the scale without affecting the other. Moreover, the weight of convergence in scale evolution in sarcopterygians has been highlighted; the loss of cosmine in the vast majority of the Devonian groups is among these convergent traits. Cosmine has been shown to be a very 'flexible' combination of hard tissues with an important morphofunctional and physiological component. When considering the convergent loss of cosmine with regard to the stratigraphical distribution of the taxa, a pattern emerges: cosmine was lost independently in the majority of sarcopterygian clades during the Early to Middle Devonian. However, the reasons for this remain unclear. Further studies should focus on the environmental constraints and global climatic variations during the Devonian and check whether the loss of odontogenic components of the dermal skeleton is somehow related to changes in the ionic content of marine and/or fresh waters.

The study of the squamation in the porolepiform *Heimenia ensis* (Paper I) has shown that the pronounced growth of the overlapped areas of the scales seems to have played a major role in the morphological transition from a rhombic to rounded scale morphotype in sarcopterygians. Although the study was restricted to porolepiforms, a similar scenario could also be applied to other osteichthyans groups were this morphological transition of the squamation also occurs. The condition of *Heimenia* illustrates that the pattern of transformation from rhombic to rounded scales might have taken place from the anterior to the posterior region of the body, thus suggesting that derived character states related to squamation in osteichthyans generally begin in the anterior region, whereas the rear and fin regions retain the primitive states.

The new histological and morphological data on the scales of the Devonian tetrapod *Tulerpeton curtum* (Paper III) show that post-Devonian tetrapods inherited the bone tissue characteristics and growth pattern of the scales of aquatic early tetrapods. The ventral (gastral) scales of all post-Devonian tetrapods, whether ovoid, spindle-shaped or secondary 'squared', can thus be traced back to a simpler, rounded to ovoid morphotype, similar to that of *Tulerpeton*. Comparison with scales of other tetrapodomorph fishes suggests that histological differences between the plesiomorphic 'fish-like' sarcopterygian scale condition and the derived 'tetrapod-like' scale condition arose during the Devonian in an aquatic environment and were maintained and essentially unmodified in tetrapods during their definitive establishment on land in the Carboniferous.

Finally, scales should not be deemed as poorly informative structures in the study of early vertebrates, and particularly osteichthyans. The scales of sarcopterygians have proven to posses a valid systematic and phylogenetic value, and their study should be viewed as a useful tool in future evolutionary, paleobiogeographic, and faunal

analyses (Paper II). Taxonomic determination should be based on the presence of different, but associated, scale features (e.g., external shape, ornamentation, microstructure) rather than on unique 'distinctive' characters (which can be regarded as strongly homoplastic) (e.g., lack of cosmine, rounded shape).

**THE FIN RAYS** – The diversity of fin ray morphologies in sarcopterygians has been reviewed and presented in detail (Paper IV). The consideration of developmental modifications as responsible for this structural diversity has led to the establishment of a new framework of study, in which morphological and developmental variations of the fins and fin rays in osteichthyans should be interpreted and described under three developmental axes (proximo-distal, antero-posterior, and contralateral). A lepidotrichium can be considered as an evolutionary unit and a redefinition of a 'Fin Ray Patterning Module' for osteichthyans is currently in progress. Interactions at the molecular level (e.g., tuning and/or downregulation of genetic pathways) and anatomical level (e.g., interray width, position of the ray within the fin) could be surveyed in order to explain the variations in the lepidotrichial pattern of segmentation and bifurcation.

The question of the homology between scales and lepidotrichia has been reconsidered. New observations have evidenced that the middle vascular layer (spongiosa) made of parallel-fibered bone of the scales is homologous to the bony tissue of the lepidotrichia. Lepidotrichia do not have a basal layer (isopedine), however they can show cosmine and other odontogenic products in certain taxa that also possess similar odontogenic tissues on their scales and dermal bones. Lepidotrichia are not modified scales, although both structures share similar developmental features that suggest a deep homology of their morphogenetic system.

The loss of fin rays in tetrapods has been considered under a new evolutionary hypothesis accounting for the differential loss of the lepidotrichia in the paired vs. the median fins, the loss of bifurcation and segmentation of the lepidotrichia, and the retention of the fin rays in the caudal fin of Devonian tetrapods. The establishment of the 'Fin Ray Patterning Module' explaining the modifications of the lepidotrichia throughout the evolutionary history of tetrapodomorphs suggests that the trend towards a more developed endoskeletal component of the paired fins could be linked to the diminishing importance and progressive distalization of the fin rays. Therefore, the loss of the lepidotrichia in tetrapods can be viewed as an inherent developmental process of distalization and loss of structures in the paired and median appendages (limbs and fins). The retention of a fish-like tail supported by fin rays in Devonian tetrapods (e.g., *Acanthostega* and *Ichthyostega*) suggests that the caudal region of fishes might be more resilient to morphological changes, probably due to its vital importance in aquatic locomotion since the earliest ontogenetic stages.

## II. PERSPECTIVES

Certain issues that have been considered in this dissertation have raised a series of questions that deserve further inquiry in the years to come. The planned studies presented herein aim at contributing to the understanding of several questions of Palaeozoic vertebrate evolution in general, and to the fish-tetrapod transition, in particular.

**RHIZODONTIDS AND THE INITIAL RADIATION OF TETRAPODOMORPHS** – Rhizodontids are one of the most puzzling groups of tetrapodomorphs. However, completely preserved rhizodontid bodies are scarce and thus many important aspects of their early evolution remain elusive. In order to better understand their anatomy and phylogenetic relationships (both within the group and with other tetrapodomorphs) the following two studies are planned:

**1.** A new rhizodontid from the Late Devonian (Famennian) of the Red Hill site (Philadelphia, USA) is currently being described with co-authors (Edward DAESCHLER, Martin BRAZEAU, and Gaël CLÉMENT). This exquisitely preserved material shows an interesting mix of features that would place it among the most basal rhizodontids. The scales and lepidotrichia are preserved to a great extent and their distinctive features might shed more light in the evolutionary modifications of the fin rays in rhizodontids. Indeed, the earliest rhizodontid *Goologoongia* has long and unsegmented rays in the pectoral fins but 'normally' segmented rays in the median fins (JOHANSON & AHLBERG, 2001), whereas in more derived forms all lepidotrichia are long and unjointed in all fins. In this new form from USA, the lepidotrichia of the caudal and dorsal fins are normally segmented, but some could show a slight distalization of the segmentation. The scales are of the 'rhizodontid-type', but show a posterior pointed end, similar to that of certain scales of *Goologoongia*.

**2.** The presence of cosmine in the scales of the putative rhizodontid *Thysanolepis* from the Late Devonian of Russia begs for a revision of the tetrapodomorph material of the PIN in Moscow (in collaboration with Oleg LEBEDEV). Re-examination of the *Thysanolepis* remains and "osteolepiforms", comprising large lower jaws and other cranial and dermal material would be most interesting and might probably confirm the proposed attribution of *Thysanolepis* to the Rhizodontida (COATES & FRIEDMAN, 2010).

Phylogenetic analyses on this material might precise the still debated phylogenetic position of rhizodontids among tetrapodomorphs.

**COSMINE, SCALES, AND LEPIDOTRICHIA** – The survey of the different occurrences of cosmine in sarcopterygians has highlighted the structural diversity of the cosmine (and other associated histological layers) and the developmental relationships between scales and fin rays. Two studies are planned to complete my previous observations:

**1.** A fin base fragment of *Porolepis* (MNHN.f. SVD 4319 A/B) from the early Devonian of Spitsbergen was scanned using synchrotron radiation by Sophie SANCHEZ at the ERSF. I have already initiated the 3D modelling of the specimen under VG Studio Max (see Discussion, fig. V.1). This study, currently in preparation with co-authors (Per AHLBERG, Sophie SANCHEZ, and Gaël CLÉMENT) aims at reconstructing the fine structure of the cosmine and the architecture of the vertical and horizontal canals in this "porolepidid". Moreover, I also plan to tackle the relationships between scales and lepidotrichia at the base of the fin and check the extension of the unjointed proximal portion of the lepidotrichia. Based on my personal suppositions, this portion of the lepidotrichia will not show cosmine, thus enabling to study the conditions of 'apposition' of cosmine in the exposed areas of the fin scales and distal lepidotrichial segments.

**2.** Scale material of *Megalichthys* (ANSP, 2009, unnumbered) from the Late Devonian of the Red Hill site (Philadelphia, USA) has been recently CT-scanned by Miguel GARCÍA SANZ at the MNHN. The data are ready to begin the post-treatment and three-dimensional virtual reconstruction phase (although a complementary scan by synchrotron radiation might be useful). In this study with co-authors (Edward DAESCHLER and Gaël CLÉMENT) I shall also focus on the reconstruction of the fine structure of the cosmine and the arrangement of the vertical and horizontal canals. The results

will then be compared with those of *Porolepis*, as previously described. Both projects aim to compare the virtual microtomographical reconstructions with former schematical (and possibly 'idealistic') representations of the arrangement of the pore-canal system of the cosmine (e.g., GROSS, 1956; THOMSON, 1975).

**THE DEVONIAN OF SPAIN** – The Devonian is not among the best represented periods in the geological register of the Iberian Peninsula (e.g., CARLS, 1988), however, numerous Devonian vertebrate-yielding sites have been discovered and studied in recent years by a team led by Hector BOTELLA (UV). The Early and Middle Devonian of Spain has yielded a diverse marine fauna, comprising "agnathans" (e.g., BOTELLA *et al*., 2006), placoderms (e.g., DUPRET *et al*., 2011), "acanthodians" (e.g., MADER, 1986), chondrichthyans (e.g., BOTELLA, 2006), but also sarcopterygians (SCHULTZE, 1973). However, most of the material consists of isolated microremains, such as scales and fin spines. Nevertheless, to my knowledge, the most complete vertebrate specimen corresponds to the skull of the onychodontid *Grossius aragonensis* from the Middle Devonian of Aragón (North-eastern Spain) (SCHULTZE, 1973). The state of preservation of the *Grossius* specimen is excellent, and I had the chance to examine it during my stay at the MB, Berlin. This specimen was the only one ever extracted from the quarry, and therefore, the possibility of finding further onychodontid, or other sarcopterygian remains in the same region is relatively high. My interest in continuing the survey of Devonian fossil sites in Spain, and especially sarcopterygian-yielding sites (probably Late Devonian ones), is shared by Hector BOTELLA and Martin BRAZEAU, and field trip collaborations have already been considered.

**EVOLUTION OF THE DERMOSKELETON IN SARCOPTERYGIAN FISHES AND EARLY TETRAPODS** – Research in this broad topic needs to be continued using the starting hypothesis and laboratory experiments developed in this thesis. These studies are intended to be pluridisciplinar, including palaeontology and developmental biology under the evo-devo approach. Among the possible studies to be performed, I have developed the two following ones with the help of different collaborators. Both projects have been submitted as Post-Doctoral Research Projects to different fellowships:

**1.** The sequential loss of the dermoskeleton during the fish to tetrapod transition will be investigated based on the establishment of the 'Fin Ray Patterning Module' (as will be detailed in Paper IV). The differential losses of fin rays in the limbs versus tail, and the scales, from various parts of the body will be evaluated in order to determine whether this condition is related to an expanded fin endoskeleton. The morphological diversity of the fossil and extant osteichthyan trunk dermoskeleton shall be characterized, combining classical and powerful new methodologies. The observations will then be interpreted in the light of developmental data from the zebrafish paired and median fins. This multidisciplinary project has been submitted as a Research Program to the Marie Curie Intra-European Fellowship (collaboration with Zerina JOHANSON, scientist in charge of the project at the Natural History Museum, London).

**2.** The evolution of scales and the respiratory apparatus during the fish-tetrapod transition will be explored by gathering information on the importance of scales (and their derivatives), gills, and lungs in the respiratory strategies of basal tetrapods and their closest fish relatives. The obtained morphological and functional data concerning gastral scales/gastralia, rib morphology and the choanae (or internal nostrils) will be compared to detect which of these characters might be functionally correlated. These aspects are crucial in our understanding of the physiological changes that took place

during the transition to land of early tetrapods and the early evolution of amniotes. This multidisciplinary project is ready to be submitted as a Research Plan to the Alexander Von Humboldt Research Fellowship (collaboration with Florian WITZMANN, host at the Museum für Naturkunde, Berlin).

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# APPENDICES

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**APPENDIX I.** Papers

The following papers were written during the course of my thesis but are not part of this Ph.D dissertation:

**V** **Mondéjar-Fernández, J.** 2011. L'origine des tétrapodes et la sortie des eaux [*The origin of tetrapods and the transition to land*]. *Découverte, Revue du Palais de la Découverte,* 372: 20-29.

**VI** Davesne, D., **Mondéjar-Fernández, J.**, Hairapetian, V., Rücklin, M., Wendt, J. & Clément, G. A new tetrapodomorph sarcopterygian from the Devonian of Iran. Considering submission to *C. R. Palévol, Acta Palaeontologica Polonica*.

**Poster** Davesne, D., **Mondéjar-Fernández, J.**, Hairapetian, V., Rücklin, M., Wendt, J. & Clément, G. 2011. Remains of a large non-tetrapod tetrapodomorph (Vertebrata, Sarcopterygii) from the Zarand Formation (Upper Devonian) of Southeastern Iran; pp: 29-30 *in Abstracts of the II International Obruchev Symposium on Palaeozoic Early Vertebrates*, St Petersburg, Russia, August 2011.

In Paper V, I wrote the article, and produced all the squematical reconstructions; pictures and drawings were courtesy of Raúl MARTÍN (Figs. 0, 2, and 5), Jennifer CLACK (Figs. 7,8, and 9), and Per AHLBERG (Fig. I). In Paper VI, I performed the 3D reconstruction of the specimen, greatly contributed to the writing along with Donald DAVESNE, and shared the interpretation and discussion of the results with the other co-authors. In the Poster I contributed to the discussions and shared the interpretation and discussion of the results with the other co-authors.

# Paper V

# L'ORIGINE DES TÉTRAPODES

## Et la sortie des eaux

Il y a près de 380 millions d'années s'est produit l'un des épisodes les plus importants dans l'histoire des vertébrés : l'émergence des tétrapodes. Cette transition évolutive qui fascine les paléontologues est de mieux en mieux comprise grâce à la découverte de nouveaux fossiles. Nous allons remonter le temps jusqu'au Dévonien pour présenter les grandes étapes de l'évolution de ces premiers vertébrés à quatre pattes.

PAR **JORGE MONDÉJAR FERNÁNDEZ,** DOCTORANT EN PALÉONTOLOGIE AU MUSÉUM NATIONAL D'HISTOIRE NATURELLE DE PARIS

L'émergence des tétrapodes est une étape majeure de l'évolution des vertébrés car ces premiers animaux à « quatre pattes » munies de doigts sont à l'origine de l'ensemble des vertébrés terrestres actuels, depuis les amphibiens et les reptiles jusqu'aux oiseaux et aux mammifères. Comprendre leur évolution permet de connaître une partie de notre lointain passé puisque nous sommes également des tétrapodes terrestres. Depuis plus de un siècle, les scientifiques essaient de déchiffrer la « sortie des eaux », c'est-à-dire la transition évolutive entre les poissons et les tétrapodes. Pour ce faire, nous devons nous intéresser à un groupe particulier de poissons osseux du Dévonien : les sarcoptérygiens.

### Les Sarcoptérygiens, des poissons pas comme les autres

Le Dévonien (–416 à –360 millions d'années) est connu traditionnellement comme « l'âge des poissons ». Parmi les nombreux groupes de vertébrés aquatiques de l'époque, se trouve celui des sarcoptérygiens. Le nom sarcoptérygien provient du grec *sarx* qui veut dire chair et de *pteryx*, la nageoire ou l'aile. « Sarcoptérygien » signifie donc nageoire charnue. En effet, ces poissons se caractérisent notamment par la présence dans les nageoires paires d'une articulation singulière, dite monobasale, formée par un seul os (humérus ou fémur) attaché à la ceinture pectorale (épaule) ou pelvienne (bassin). Cette articulation accroît l'amplitude des mouvements et favorise le développement d'une importante musculature. L'organisation des os à l'intérieur de cette nageoire charnue rappelle l'architecture de nos membres et constitue un schéma précurseur de la patte porteuse caractéristique des tétrapodes terrestres (fig. 1). La nageoire monobasale composée majoritairement d'os permet ainsi de différencier les sarcoptérygiens de l'autre grand groupe de poissons osseux, les actinoptérygiens. Ces derniers possèdent des nageoires formées principalement de rayons et comprennent la quasi-totalité des espèces de poissons actuels (comme la morue, le thon ou le poisson rouge).

Jadis très diversifiés au Dévonien, les sarcoptérygiens ne sont représentés dans la nature actuelle que par trois groupes : les cœlacanthes (deux espèces), les dipneustes (six espèces) et les tétrapodes (environ 24 000 espèces). Malheureusement, les cœlacanthes et les dipneustes sont trop éloignés des tétrapodes pour comprendre en détail comment ces

→→→

Reconstitution d'*Acanthostega*, un tétrapode vieux de 365 millions d'années, évoluant dans un milieu aquatique peu profond et encombré de débris végétaux de la fin du Dévonien. © R. Martín.

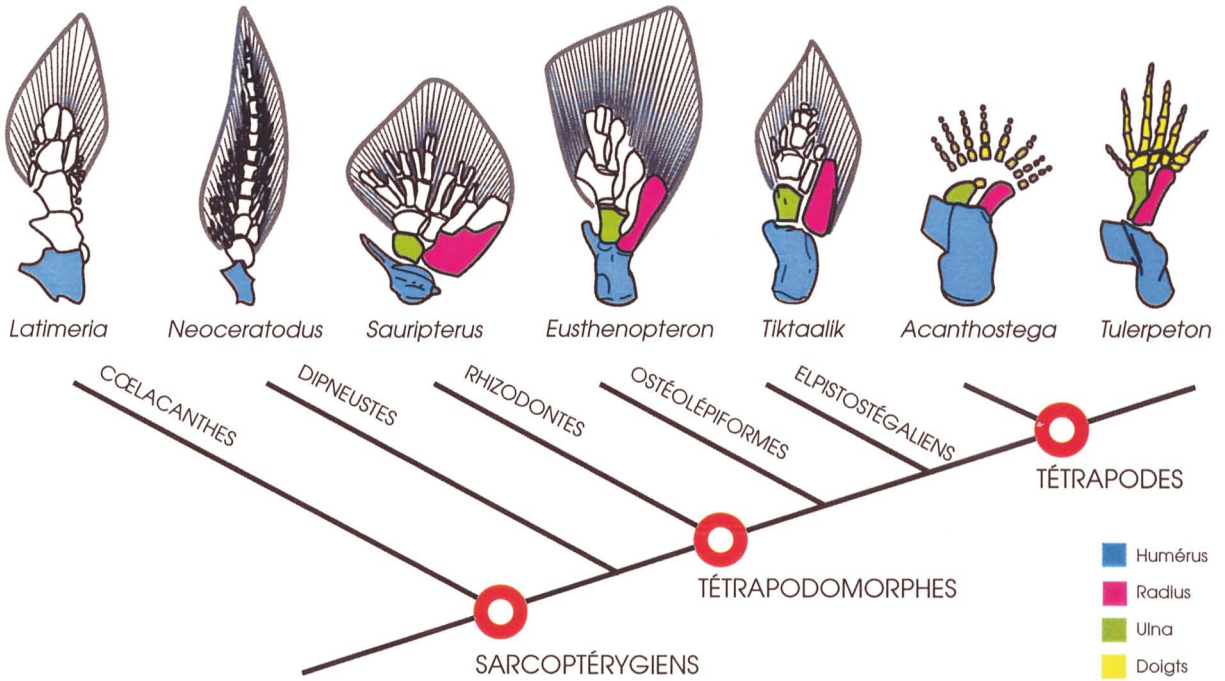


**Figure 1.** Cladogramme (ou arbre phylogénétique) illustrant les relations de parenté et l'évolution des nageoires au sein des poissons sarcoptérygiens. © J. Mondéjar Fernández.

derniers sont apparus. Pour connaître leur origine, nous devons nous pencher sur des groupes fossiles de sarcoptérygiens dévoniens, et plus particulièrement sur le groupe des tétrapodomorphes.

## Les tétrapodomorphes, des presque tétrapodes ?

Les poissons tétrapodomorphes forment le groupe incluant les plus proches parents fossiles des tétrapodes et les tétrapodes eux-mêmes (fig. 1). Ces « poissons à forme de tétrapodes » du Dévonien moyen et supérieur constituent ce qu'on appelle en paléontologie des « formes de transition ». Leur étude nous permet de mieux comprendre la séquence d'acquisition des caractères distinctifs des tétrapodes.

### EUSTHENOPTERON, UNE HISTOIRE REVISITÉE

Parmi les fossiles de poissons tétrapodomorphes les plus complets et les mieux connus se trouve *Eusthenopteron* datant du Dévonien supérieur (–385 millions d'années) et découvert dans la baie de Miguasha (Québec). Pendant longtemps, cet ostéolépiforme (fig. 1) fut considéré comme un « prététrapode », adapté aussi bien à la vie aquatique que terrestre. Dans les anciens manuels scolaires, on représentait *Eusthenopteron* rampant péniblement sur le sol avec ses nageoires charnues suite à l'assèchement périodique des mares où il habitait. Pour survivre, il aurait été « forcé » de se déplacer sur terre avec ses nageoires à la recherche de cours d'eau plus profonds. Progressivement, les poissons comme *Eusthenopteron* auraient fini par développer des pattes. D'après cette interprétation, les pattes seraient apparues pour retourner à l'eau !

Aujourd'hui, ce scénario trop réductionniste est rejeté depuis longtemps par les scientifiques. Malgré la structure de ses nageoires, *Eusthenopteron* ne saurait être capable de se déplacer sur la terre ferme ! (fig. 2). Néanmoins, bien qu'il possède des caractères de type ichthyen, comme un corps fusiforme, des écailles et une nageoire caudale, il présente aussi de nombreux attributs de tétrapode. Parmi eux citons notamment des choanes (ou narines internes), sans doute des poumons fonctionnels permettant de respirer l'oxy-

**Figure 2.** Reconstitution d'*Eusthenopteron*, un poisson sarcoptérygien tétrapodomorphe du Dévonien moyen. © R. Martin.

gène de l'air et une organisation des os des nageoires identique à celle des pattes des tétrapodes (avec humérus-radius-ulna pour le membre antérieur, et fémur-tibia-fibula pour le membre postérieur) (fig. 1 et 8). *Eusthenopteron* est donc un bon exemple d'évolution en mosaïque où certains caractères évoluent plus vite que d'autres.

## TIKTAALIK, DES NOUVELLES DE L'ARCTIQUE

L'évolution des poissons tétrapodomorphes est riche en formes qui montrent une certaine « prédisposition » à la vie sur terre. C'est le cas du groupe des elpistostégaliens, les tétrapodomorphes les plus proches parents des tétrapodes (fig. 1). Ces poissons, au nom particulièrement imprononçable, partagent de nombreux caractères anatomiques avec les premiers tétrapodes, comme la perte des nageoires dorsales et anale et la présence d'orbites situées au sommet d'un crâne aplati. Ils ne sont représentés que par trois genres fossiles du Dévonien moyen et supérieur : *Elpistostege*, *Panderichthys* et *Tiktaalik*. Ce dernier, le plus récemment découvert, est aussi le plus intéressant.

*Tiktaalik* fut exhumé en 2004 dans l'île d'Ellesmere, dans l'Arctique canadien (fig. 3) dans des roches du Dévonien supérieur (–375 millions d'années). Ce « grand poisson des rivières » (en dialecte inuit) illustre bien l'étape intermédiaire entre les vertébrés aquatiques et terrestres. Comme tout bon poisson, il conserve une couverture d'écailles et des rayons à l'extrémité des nageoires paires. Mais il présente aussi presque tous les attributs →→→

**Figure 3.** Fossile de *Tiktaalik*, un poisson elpistostégalien proche parent des tétrapodes. © M. Mechtley.

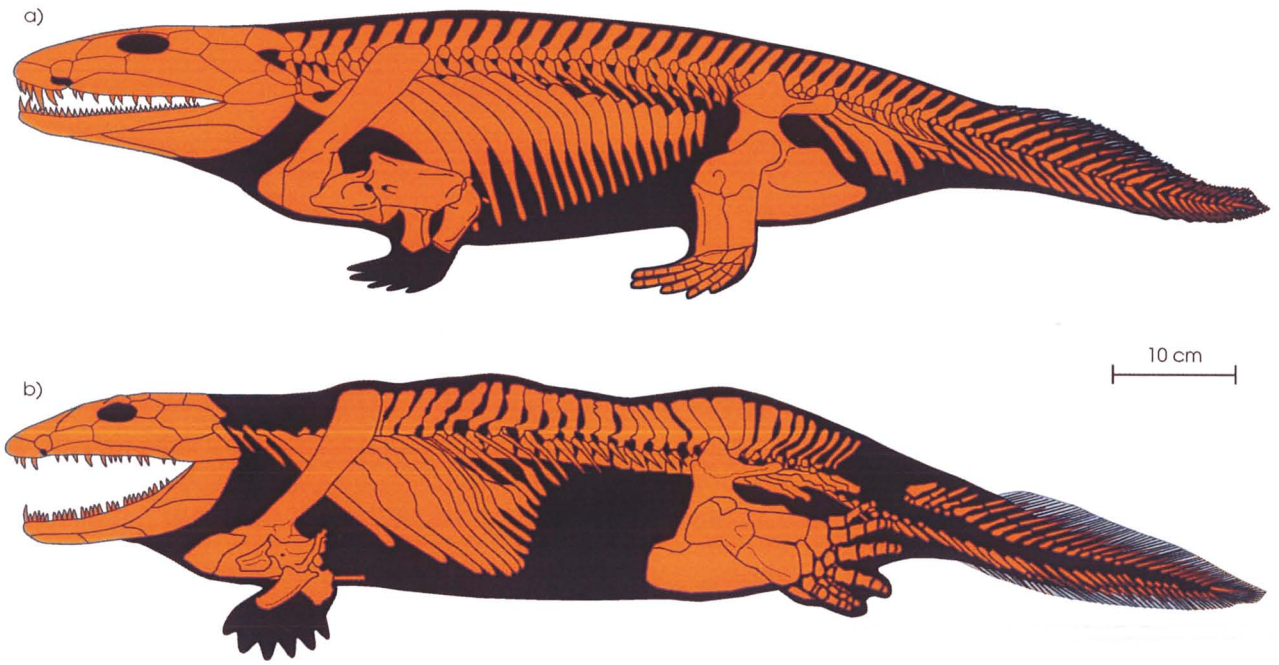


**Figure 4. Squelettes d'*Ichthyostega*, un tétrapode mythique de la fin du Dévonien. a) Ancienne représentation d'*Ichthyostega* comme une « grosse salamandre ». b) Nouvelle vision d'*Ichthyostega*.** © J. Mondéjar Fernández, d'après P. Ahlberg et al. (2005).

→→→

qui définissent les tétrapodes, à l'exception des doigts ! En effet, *Tiktaalik* possède un cou séparant le crâne des épaules. Il lui aurait permis de relever la tête hors de l'eau pour se nourrir d'invertébrés terrestres et respirer. Or, la présence du cou était auparavant un caractère exclusif aux tétrapodes. Voilà qu'avec *Tiktaalik* le cou passe du côté des poissons ! De plus, l'articulation des os à l'intérieur de ses nageoires pectorales robustes, mais encore munies de rayons, auraient permis à *Tiktaalik* de mieux soulever son corps sur les berges des rivières peu profondes.

## Les premiers tétrapodes... aquatiques !

La découverte de nouveaux fossiles de sarcoptérygiens dévoniens a comblé quelques lacunes dans notre connaissance de l'évolution des tétrapodes. Du point de vue anatomique, nous remarquons qu'il n'y a pas eu de grands sauts entre les différents groupes (comme entre *Eusthenopteron* et *Tiktaalik*), mais plutôt une continuité anatomique ponctuée par quelques modifications structurales précises (par exemple l'apparition du cou ou la réduction des rayons des nageoires). En effet, presque toutes les structures anatomiques qui rendront possible le développement des vertébrés sur terre sont déjà présentes chez les poissons tétrapodomorphes. Quand on considère les fossiles, la frontière qui sépare les poissons des tétrapodes devient de plus en plus floue. Néanmoins, un seul caractère est exclusif aux tétrapodes et permet de les séparer clairement des formes ichthyennes : les doigts.

### ICHTHYOSTEGA, UN TÉTRAPODE MYTHIQUE

Au début du XX$^{e}$ siècle, les scientifiques ne disposaient que de quelques fossiles illustrant la transition entre les poissons et les vertébrés terrestres, le plus important étant *Eusthenopteron* qui, du côté des formes ichthyennes, était considéré comme un premier « essai » de la sortie des eaux. Il leur manquait toutefois un fossile essentiel pour confirmer que l'ori-

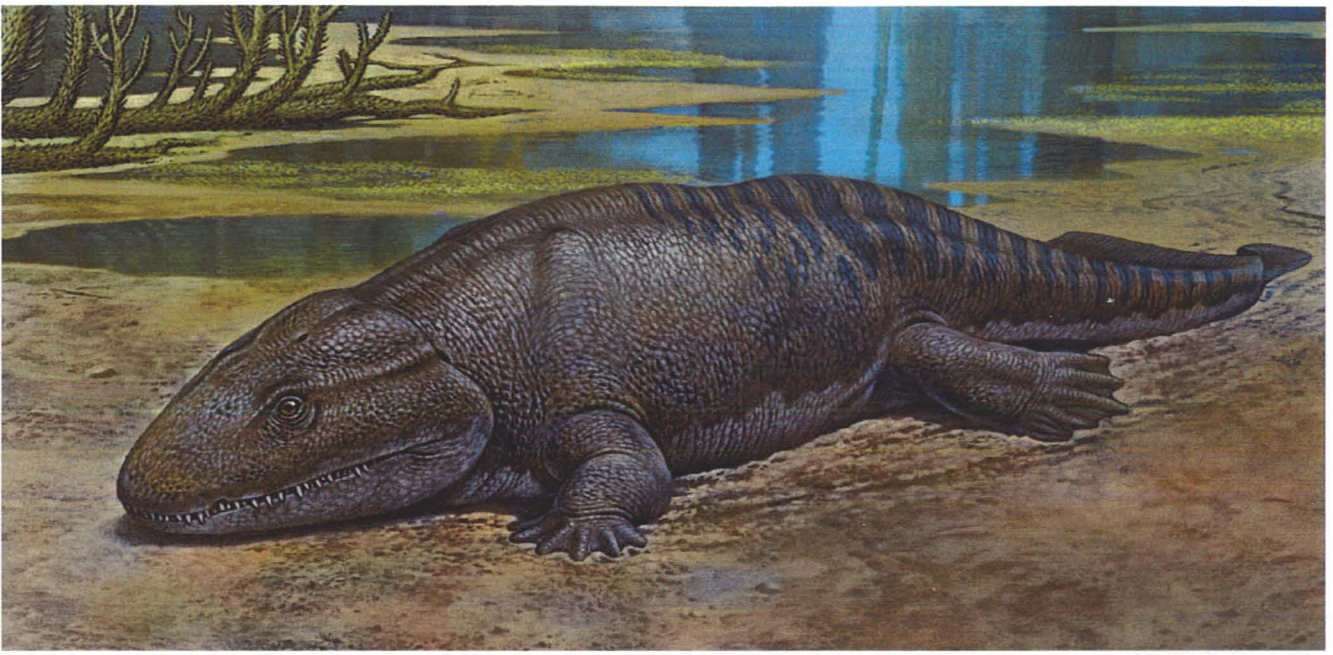

**Figure 5. Reconstitution d'*Ichthyostega* d'après les nouvelles études.** © R. Martín.

gine des tétrapodes se trouvait parmi les poissons sarcoptérygiens du Dévonien : celui du premier animal à quatre pattes. Avec la découverte au Groenland, dans les années 1950, de squelettes presque complets d'*Ichthyostega** datant du Dévonien supérieur (–365 millions d'années) tout semblait prendre sens. *Ichthyostega* est l'un des premiers tétrapodes puisqu'il possède des doigts bien visibles au pied (fig. 4 et 8) mais, malheureusement encore inconnus sur la main. Il conserve néanmoins des branchies, des écailles sur le ventre et des rayons dermiques sur la nageoire caudale, hérités de ses ancêtres aquatiques. Malgré ces caractères de poisson, *Ichthyostega* fut longtemps considéré comme le premier vertébré terrestre, capable de supporter son poids hors de l'eau et de se déplacer sur la terre ferme. La reconstitution emblématique d'*Ichthyostega* comme une grosse salamandre se fondait sur des caractères typiques d'organismes terrestres, comme une ceinture pelvienne attachée à la colonne vertébrale, une plus grande robustesse des membres et la présence de doigts. Mais des études récentes réfutent cette vision d'*Ichthyostega* (fig. 4). Les études détaillées de sa colonne vertébrale, de sa cage thoracique et de l'orientation de ses pattes arrière démontrent qu'il était un animal principalement aquatique. Il pouvait sans doute se traîner sur le sol, mais il ne pouvait pas se hisser sur ses membres. Sur terre, *Ichthyostega* devait plutôt se déplacer grâce à des mouvements ondulatoires verticaux, à la façon des phoques actuels (fig. 5). Ainsi, chez *Ichthyostega* les pattes ne participaient pas directement aux déplacements sur la terre ferme.

## ACANTHOSTEGA, UNE NOUVELLE VISION DES TÉTRAPODES

La découverte d'un deuxième tétrapode contemporain d'*Ichthyostega* dans les années 1930 et sa redescription dans les années 1990 sont venues remettre en cause de nombreuses idées reçues sur ces

* La première découverte de restes d'*Ichthyostega* se situe dans les années 1930.

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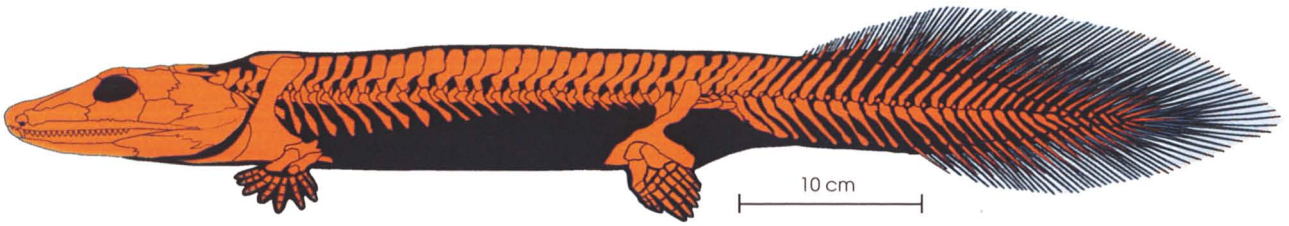


**Figure 6. Squelette d'*Acanthostega*, le tétrapode dévonien le plus complet retrouvé à ce jour.**
© M. Rotaru et J. Mondéjar Fernández, d'après P. Ahlberg et al. (2005).

animaux. *Acanthostega*, datant du Dévonien supérieur et découvert également au Groenland, est le tétrapode dévonien le plus complet retrouvé à ce jour (fig. 6). L'étude de son squelette nous a apporté bon nombre de surprises... *Acanthostega* possède non seulement des branchies, des écailles sur le ventre et une nageoire caudale avec des rayons, comme *Ichthyostega*, mais cette dernière est longue, effilée et symétrique (fig. 7) ! Avec une telle nageoire et des membres aussi courts, c'est impossible d'imaginer *Acanthostega* comme un animal terrestre. De plus, sur ses mains et ses pieds très bien conservés les chercheurs ont mis en évidence... huit doigts ! Avant cette découverte, tous les scientifiques s'accordaient à dire que la patte des tétrapodes primitifs n'avait que cinq doigts au maximum. Désormais, nous devons abandonner cette idée car, suite à cette découverte inattendue chez *Acanthostega*, les doigts d'*Ichthyostega* furent revus et recomptés et, nouvelle surprise, ils n'étaient pas cinq mais sept (fig. 8) ! De même, *Tulerpeton*, un autre tétrapode découvert en Russie et datant du Dévonien supérieur, présente six doigts sur le membre postérieur (fig. 1) !

Grâce à ces nouvelles observations sur le nombre de doigts et aux études sur l'orientation des pattes par rapport au corps, l'on sait que les membres des premiers tétrapodes n'étaient pas des pattes porteuses, mais plutôt des palettes natatoires adaptées à la vie dans l'eau. Il s'agit là d'un exemple clair d'exaptation (ou préadaptation), dans lequel un organe à l'origine utile pour une fonction (ici la nage) est utilisé secondairement au cours de l'évolution pour une autre fonction (la marche). L'ancienne idée selon laquelle les pattes seraient apparues chez les premiers tétrapodes dans le but précis de marcher doit être rejetée. Les pattes ne sont pas apparues lors de la sortie des eaux mais sans doute quelques dizaines de millions d'années avant !

**Figure 7. Fossile d'*Acanthostega*.**
© J. Clack.


## La fin du Dévonien et l'apparition des tétrapodes terrestres

Depuis les redescriptions d'*Ichthyostega* et d'*Acanthostega* et la découverte de nouveaux fossiles dans les années 1990 et 2000, la recherche paléontologique sur les premiers tétrapodes a connu une renaissance. Aujourd'hui nous connaissons treize espèces de tétrapodes dévoniens largement

Pour aller plus loin

# Une découverte révolutionnaire

**Un des aspects fondamentaux pour comprendre l'origine des tétrapodes consiste à savoir dans quels écosystèmes ces animaux ont évolué.** Aujourd'hui, on admet que le Dévonien était une période très verte et jouissant d'un climat tropical. Les plantes avaient réalisé leur sortie des eaux bien avant le Dévonien et occupaient déjà une grande partie des terres émergées. Grâce à la stabilisation des sols par les racines des premières fougères arborescentes et des plantes à graines, de nouveaux écosystèmes forestiers se développèrent. Un climat à saisonnalité marquée et des apports continus en matière organique végétale auraient fait des milieux aquatiques continentaux des écosystèmes riches en biodiversité. C'est dans ces marais d'eau douce peu profonds et encombrés de débris végétaux de la fin du Dévonien que les premiers tétrapodes seraient apparus (figure p. 20). Cependant, ce scénario vient d'être chamboulé par une découverte extraordinaire. Des empreintes de pas datées du Dévonien moyen (–395 millions d'années) ont été découvertes en Pologne au début de l'année 2010 (fig. I). Ces traces n'ont pu être produites que par des animaux à quatre pattes, c'est-à-dire des tétrapodes, très anciens... même « trop » anciens puisque leurs plus vieux ossements datent du Dévonien supérieur (–377 millions d'années) ! Ces empreintes reculent l'apparition des tétrapodes d'au moins 18 millions d'années ! De plus, elles seraient au moins 10 millions d'années plus vieilles que les plus anciens restes fossiles d'elpistostégaliens, leurs plus proches parents ! Ces traces ont bouleversé la datation de l'origine des tétrapodes et révolutionné aussi nos idées sur le type d'environnement dans lequel ils seraient apparus. En effet, les roches qui contiennent ces empreintes sont caractéristiques d'une lagune marine peu profonde. Les tétrapodes, longtemps considérés comme des animaux apparus dans des milieux marécageux d'eau douce, montrent donc, depuis leurs tout premiers pas évolutifs, une grande tolérance aux variations de salinité et une diversité considérable dans leur mode de vie. Quelles nouvelles surprises nous réserve le registre fossile de ces premiers tétrapodes ?

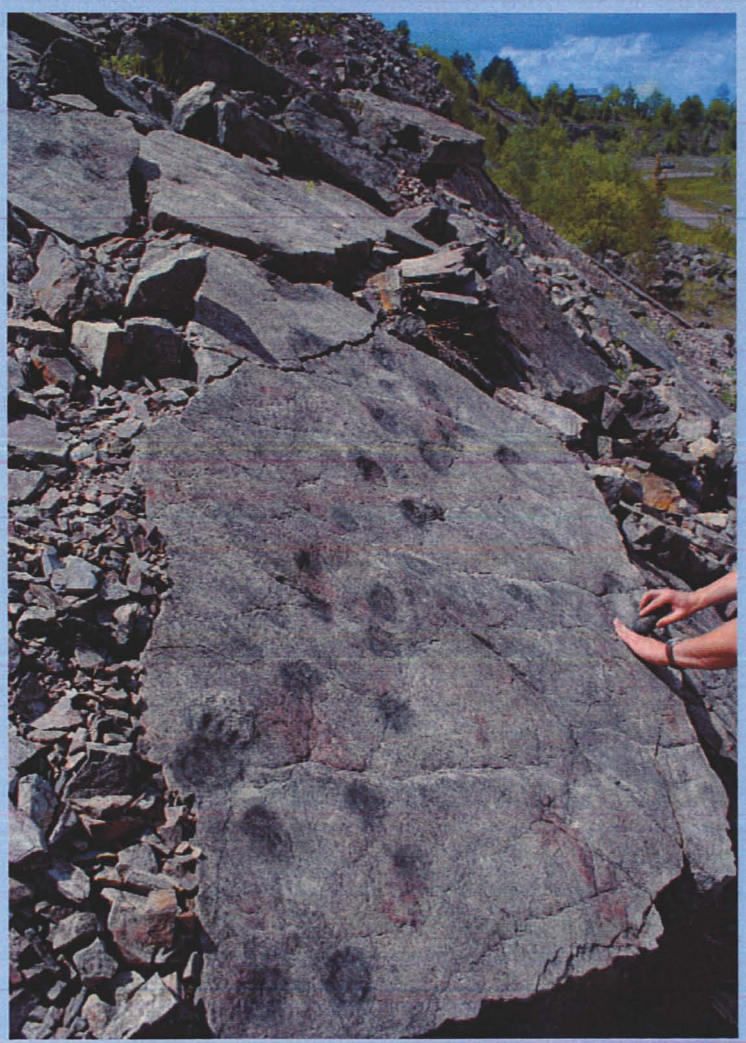

**Figure I. Des traces de pas récemment découvertes dans le Dévonien moyen de Pologne.** © P. Ahlberg.

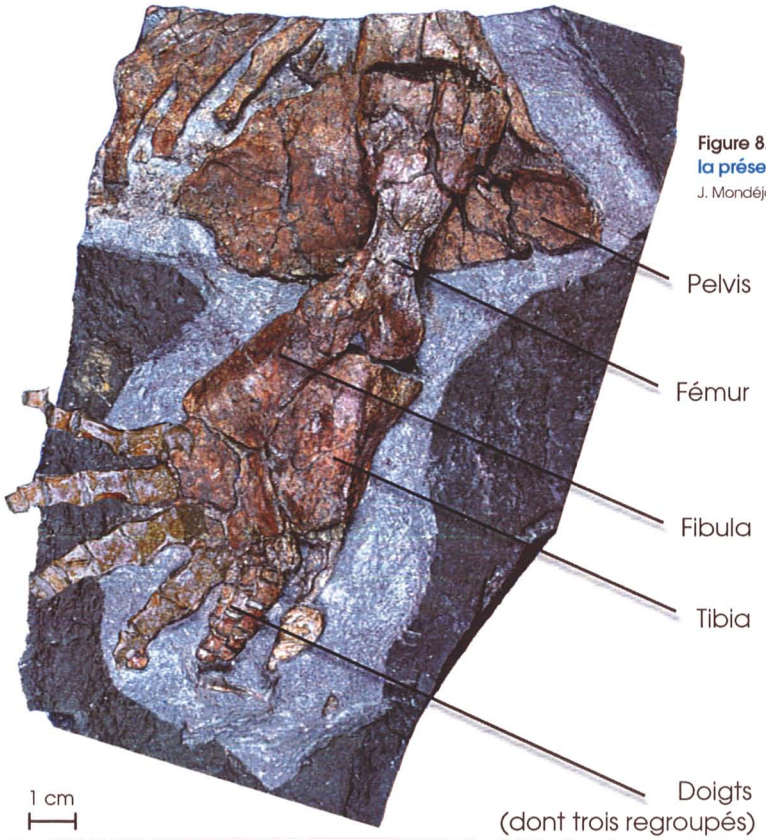


**Figure 8. Patte arrière d'*Ichthyostega* illustrant la présence de 7 doigts.** © J. Clack, modifiée par J. Mondéjar Fernández.


## Jorge Mondéjar Fernández

**Jorge Mondéjar Fernández est doctorant en paléontologie au Muséum national d'histoire naturelle de Paris où il étudie l'origine des tétrapodes.** Ses recherches portent sur les écailles et les nageoires des sarcoptérygiens en associant les points de vue de la paléontologie et la biologie du développement. Ayant participé à de nombreuses fouilles, il transmet sa passion pour la paléontologie au travers d'exposés et ateliers qu'il anime pour le département des sciences de la Terre du Palais de la découverte.


distribuées sur l'ensemble du globe, ce qui suppose une grande diversité de formes et de modes de vie de ces animaux. Cependant, des débats et des questions subsistent sur les environnements et la date d'apparition des tous premiers tétrapodes (encadré *Une découverte révolutionnaire*). La grande majorité des espèces dévoniennes sont considérées comme des formes principalement aquatiques. Il ne faut pas confondre donc l'origine des tétrapodes avec leur « terrestrialisation », c'est-à-dire leur adaptation au milieu terrestre ; cette dernière ne se produira que plus tard, au cours du Carbonifère (env. –360 à 300 millions d'années). Malheureusement, les fossiles témoignant de cette autre transition sont encore plus rares...

### LA CRISE DÉVONIEN-CARBONIFÈRE ET LA LACUNE DE ROMER

À la fin du Dévonien, il y a environ 360 millions d'années, un refroidissement et une diminution du taux d'oxygène atmosphérique provoquèrent une crise biologique qui entraîna la disparition de nombreux groupes d'organismes et toucha notamment les premiers tétrapodes. Après cette crise, les tétrapodes disparurent mystérieusement du registre fossile pendant les 20 premiers millions d'années du Carbonifère. Cette période est nommée lacune de Romer, en hommage au fameux paléontologue américain, Alfred Romer (1894-1973) qui la mit en évidence pour la première fois. L'absence de fossiles de tétrapodes durant cette période demeure un mystère. La seule exception est le petit *Pederpes* du Carbonifère inférieur (–350 millions d'années) d'Écosse (fig. 9) qui montre une certaine tendance vers la terrestrialité. Après ce *hiatus*, on trouve à nouveau des fossiles de tétrapodes, mais qui sont totalement terrestres et ne présentent plus que cinq doigts par membre. Ces nouvelles formes, très différents de celles du Dévonien, donneront naissance au cours du Carbonifère à de nombreux groupes d'amphibiens, puis de reptiles. Ce seront ces derniers qui s'affranchiront définitivement du milieu aquatique. Grâce à leurs œufs protégés par une coquille, ils pourront pondre et se reproduire sur la terre ferme et achèveront la sortie des eaux des vertébrés, près de 40 millions d'années après l'apparition des pattes !

## Un pas après l'autre...

Notre conception de la sortie des eaux a été longtemps associée à une idée de progrès et de but évolutif. Selon cette vision, les structures anatomiques se seraient complexifiées davantage dans un but précis : la conquête du milieu terrestre. Mais, précisons-le, cette idée est fausse ! Comme on l'a vu, cette transition ne correspond pas à un brusque saut évolutif. L'acquisition des caractères qui définissent aujourd'hui les tétrapodes s'est faite graduellement, étalée

Figure 9. *Pederpes*, un petit tétrapode terrestre du Carbonifère. © J. Clack.

L'idée selon laquelle les pattes auraient évolué chez les tétrapodes dans le but précis de marcher sur la terre est fausse. Les pattes ne sont pas apparues lors de la sortie des eaux mais sans doute quelques dizaines de millions d'années avant !

sur environ 25 millions d'années au cours du Dévonien. Les premiers tétrapodes étaient des formes aquatiques, incapables de vivre hors de l'eau de façon permanente. En outre, ils présentaient un ensemble de caractères à la fois primitifs (branchies, écailles et rayons des nageoires) et dérivés (cou, membres munis de doigts, etc.) ; autant de caractères hérités des poissons tétrapodomorphes dévoniens.

Malheureusement, certains chapitres de l'histoire évolutive des premiers tétrapodes demeurent encore inconnus. Toutefois, les recherches et les nouvelles découvertes en paléontologie de ces 20 dernières années ont changé complètement notre vision sur leur évolution. Elles ont également ouvert de nouveaux fronts d'étude pour mieux comprendre tous les aspects anatomiques, physiologiques et génétiques liés à la sortie des eaux. En effet, une discipline scientifique relativement récente et en plein essor liant paléontologie, biologie du développement et génétique (nommée « Évo-Dévo » pour Évolution-Développement) s'annonce prometteuse de découvertes majeures... **J. M.-F.**

# Paper VI

**A new tetrapodomorph sarcopterygian from the Devonian of Iran**

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## INTRODUCTION

The question of the biogeographic affinities of the non-tetrapod sarcopterygians is essential to propose hypothesis on the biogeographic models related to the conditions of appearance of tetrapods during the Devonian, and to discuss paleogeographic models based on early vertebrates (e.g., Young et al., 2010). Tetrapodomorph taxa, such as rhizodontids and tristichopterids, had a worldwide distribution by the Late Devonian. However, our understanding of the continental margins of Northern Gondwana during these times remains largely elusive.

Only a few Late Devonian fossil vertebrates localities are known from regions considered as part of the northern margin of Gondwana: Morocco, Afghanistan, Iraq and Iran (Blieck et al., 1982; Lelièvre et al., 1993; and references therein). Such localities have provided a diverse set of sarcopterygian remains, but tetrapodomorphs are poorly represented, except in the case of Morocco, from which several cranial remains have been assigned to an "*Eusthenopteron*-like" tristichopterid (Lehman, 1977; Lelièvre and Janvier, 1986) and Iran (Janvier and Martin, 1979). The Devonian of Iran has yielded a diverse vertebrate fauna (Golshani et al., 1973; Golshani and Janvier, 1974; Hairapetian et al., 2000) comprising thelodonts, acanthodians (Hairapetian et al., 2006), chondrichthyans (Hairapetian et al., 2008), actinopterygians, placoderms and sarcopterygians. Placoderms are well represented by several antiarchs, arthrodires and ptyctodonts (Janvier, 1979; Lelièvre et al., 1981, 1993). The sarcopterygian fauna is composed of onychodontids, actinistians (Janvier and Martin, 1979) and rhipidistians. Dipnomorphs are represented by dipnoans (Janvier, 1978) and by a putative porolepiform cleithrum. Tetrapodomorphs are only represented by isolated scales and a fragment of a cosmine-covered maxilla attributed to an undetermined ‘‘osteolepidid’’ (Janvier and Martin, 1979). More complete remains of tetrapodomorphs have never been described

from this region, and none had been referred to rhizodontids or tristichopterids until now.

Here we describe a new fossil specimen of a large non-tetrapod tetrapodomorph from the Late Devonian of Southeastern Iran, revealed by CT-scan microtomography and 3D visualization.

**Institutional Abbreviations—MNHN**, Muséum national d'Histoire naturelle, Paris, France

## MATERIAL AND METHODS

The specimen studied here, MNHN.F.URP 550, was collected during field work in 2001 by one of us (J.W.) at the Gask locality of the Kerman region, Southeastern Iran (Fig. 1). The specimen was discussed (although unnamed) by Wendt et al. (2002:138), first—by mistake from an earlier manuscript version—as an acanthodian and later corrected in the same publication as a sarcopterygian (Wendt et al., 2002:153, fig. 12).

The bone-bearing matrix is a coarse sandstone conglomerate including large quartz pebbles (Fig. 2). Externally, the bone is incompletely visible and highly microfracturated. Due to the heterogeneity of the surrounding siliciclastic matrix, a preparation using conventional, mechanical techniques was impossible. It was thus decided to study the specimen by means of X-Ray tomographic techniques (CT-scan) and 3D-visualization. A scan series was performed at the AST-RX platform, MNHN, Paris (1965 transversal slices with an inter-slice spacing of 76,61 μm). It provided the basis for a digital reconstruction (Fig. 3) using the medical visualization software Mimics (version 14.0). The good resolution of the scans also enabled the study of bone and tooth microanatomy in more detail (Fig. 4, 5).

## GEOLOGICAL SETTING

The specimen (Fig. 2) comes from the sandstones of the Gask syncline, Zarand Formation, which is considered to be Devonian in age (Wendt et al., 2002) due to the presence of Frasnian brachiopods in the upper part of the formation (Huckriede et al., 1962). According to Wendt et al. (2002:153), the Zarand Formation is probably Givetian to Frasnian of age, spanning the Middle-Upper Devonian boundary (Fig. 1). The sandstone conglomerate, found in the lower levels of the formation could have an erosional origin from a cratonic continental block. At the locality of Gask, the Zarand Formation directly overlays the Cambrian Kuhbanan Formation, showing a large geological discontinuity. On the top of the Zarand Formation another stratigraphical gap separates the Devonian formation from the beginning of the Permian Jamal Formation, marked by a paleosol (Wendt et al., 2002:fig. 12). The sedimentological model proposes that the Zarand Formation corresponds either to a shallow marine, possibly estuarine Devonian platform, or to a sebkha deposition, alternating with two episodes of marine regression that would explain the time gaps above and below the formation (Wendt et al., 2002).

## DESCRIPTION

Externally, the specimen appears as an elongate bone bearing teeth (Fig. 2), measuring around 15 cm in length. Most of the bone is hidden by the rocky matrix and only a few details are visible. Due to its external gross morphology, as well as the presence of dermal bone and relatively large teeth visible from the lingual side, the specimen was determined as an incomplete large jaw. The external surface of the jaw bone is slightly weathered, and does not have any trace of a cosmine covering.

The CT-scan acquisitions enabled us to reconstruct structures that were hidden by the matrix and provided useful informations on the bone and teeth microstructures (Fig 3, 4, 5). Thanks to these observations, we were able to identify the specimen as the left ramus of the lower jaw (the reasons for this identification will be detailed in the Systematic Attribution part). The 3D reconstruction (Fig. 3) shows an anteroposteriorly elongate jaw, with no remarkable curvature. The only preserved bones are a part of the dentary and the first two coronoids (the anterior and middle coronoid). The symphysial region is missing.

In lingual (internal) view the posterior part of the jaw fragment shows a deep groove that we interpret as the labial wall of a narrow, probably nervous canal. This canal is visible in the virtual slices (Fig. 4), running throughout the thickness of the bone.

The anterior and middle coronoids are separated by a socket (the anterior intercoronoid fossa). There is another socket in front of the first coronoid that we identify as the precoronoid fossa; it is very narrow in our specimen.

The dentary bears a single row of small, regularly spaced teeth, and a large anterior dentary fang, caught in a shedding process (one fang is growing under an older one). Lingual to the dentary, the coronoids bear larger teeth, the so-called coronoid fangs. There is one fang on the anterior coronoid, entirely preserved. The middle coronoid bears one fang pair (with both fangs distally broken) and an intervening replacement pit between the two. The CT-scan data clearly show the lack of a marginal row of small coronoid teeth.

The internal microstructure of the anterior coronoid fang was revealed by the CT-scan data (Fig. 5). This fang shows a folded structure of the dentine (i.e., plicidentine), with primary and secondary bends. The folds are increasingly complex towards the base of the teeth. In the basal part of the teeth the bone of attachment extends between the dentine folds. This combination of histological structures matches the ‘polyplocodont’ pattern, as defined by Schultze (1969a, 1970).

Due to the incompleteness of the material, we do not attempt to assign this specimen to any existing species or genus nor do we attempt to establish it as a new taxon within the sarcopterygians.

## SYSTEMATIC ATTRIBUTION

Lower jaws are among the most common fossil material in Palaeozoic sarcopterygians and can provide numerous distinctive characters. These characters comprise arrangement of the teeth along the jaw and anatomical microstructure of the teeth. Lower jaw features may carry a relatively weak phylogenetic signal compared to other cranial characters due to morphological convergence associated with strong functional constraints imposed by modes of feeding and food handling (Zhu and Yu, 2004). Nonetheless, certain key features would enable to identify with relative confidence the phylogenetic position of isolated vertebrate lower jaws such as the one described herein.

**Absence of cosmine –** Cosmine is a characteristic combination of hard tissues (bone, dentine and enamel) primitively found in all sarcopterygian dermal bones (including external jaw bones) and scales (Meinke, 1984). Cosmine has been lost independently several times, notably in actinistians (with the possible exception of *Styloichthys*), holoptychiid porolepiforms (Mondéjar-Fernández and Clément, 2012), most dipnoans (Schultze, 1969b), rhizodontids (Jeffery, 2002; Brazeau, 2005), rhizodopsids (Schultze and Heidtke, 1986), *Canowindra* (Thomson, 1973) and in all eotetrapodiforms (*sensu* Coates and Friedman, 2010), comprising tristichopterids (Ahlberg and Johanson, 1998) and elpistostegalians (*sensu* Daeschler et al., 2006). As the studied specimen lacks cosmine on its external jaw bones, it should belong to one of these groups.

**Tooth microanatomy –** Plicidentine is present in different vertebrate taxa: ginglymod actinopterygians, numerous non-tetrapod sarcopterygians (Schultze, 1969a, 1970), most of the first tetrapods (colloquially known as ‘‘labyrinthodonts’’), and several amniotes (Maxwell et al., 2011). Amongst Devonian vertebrates, plicidentine is found only in sarcopterygians, but not in onychodontids and actinistians (Vorobyeva, 1977).

The polyplocodont-type plicidentine is the most general amongst sarcopterygians as demonstrated by its presence in the stem-sarcopterygian *Psarolepis* (Yu, 1998) and the stem-dipnomorphs *Powichthys* and *Youngolepis* (Clément and Janvier, 2004); therefore it is probably a plesiomorphic state. In this context, the dendrodont-type plicidentine of porolepiforms and the labyrinthodont-type plicidentine of *Panderichthys* and tetrapods are probably a derived, modified form of polyplocodont-type plicidentine.

**Dentition pattern–** Large inner fangs, in comparison to the smaller marginal teeth, are present on both the upper (vomer, dermopalatine and ectopterygoid fangs) and lower (coronoid fangs) jaws in sarcopterygians. Exceptions to this pattern, amongst Devonian taxa, are actinistians and dipnoans (with their modified jaws, characterised by the loss of several bones), and most of the tetrapods, with their inner rows of numerous teeth of equal size (e.g. Ahlberg and Clack, 1998). The elpistostegalians *Panderichthys*, *Tiktaalik*, *Metaxygnathus* and *Ventastega* show an intermediate pattern in the lower jaw, with large fangs anteriorly and a row of equally-sized teeth on the posterior coronoid (Ahlberg and Clack, 1998; Daeschler et al., 2006).

Large fangs are sometimes present on the dentary, anteriorly to the first coronoid, in several tetrapodomorph taxa such as rhizodontids (e.g. Jeffery, 2002), *Medoevia* (Lebedev, 1995), megalichthyids (e.g. Fox et al., 1995), the tristichopterids *Eusthenodon*, *Bruehnopteron*, *Heddleichthys*, *Hyneria*, *Langlieria*, *Cabonnichthys*, *Notorhizodon* and

*Mandageria* (Thomson, 1968; Ahlberg and Johanson, 1997; Johanson and Ahlberg, 1997, 2001; Johanson, 2004; Clément et al., 2009; Snitting, 2009; Schultze and Reed, 2012), and all Devonian elpistostegalians – including tetrapods (Ahlberg and Clack, 1998). The presence of dentary fangs is homoplastic in all these taxa. For example, it is clearly a derived state amongst tristichopterids, being absent in *Spodichthys* (the sister-group to all other tristichopterids), *Tristichopterus* and *Eusthenopteron* (Ahlberg and Johanson, 1998; Snitting, 2008). Amongst the sarcopterygians with dentary fangs, the only ones that also lack cosmine are rhizodontids, tristichopterids and elpistostegalians.

Marginal rows of smaller teeth are primitively present on the coronoids, typically located between the large coronoid fangs and the marginal row of dentary teeth. A similar pattern is encountered on the palate, with rows of small teeth on the vomer, dermopalatine and ectopterygoid. The marginal coronoid teeth are absent in rhizodontids (Jeffery, 2002) and present only on the posterior coronoid in the tristichopterid genera *Eusthenodon*, *Cabonnichthys*, *Mandageria* (Ahlberg and Johanson, 1997; Johanson and Ahlberg, 1997; Johanson, 2004) and *Hyneria* (J.M.F. pers. obs.). Interestingly, the first three of these tristichopterid taxa form a clade in Snitting's (2008) phylogenetic analysis (*Hyneria* was not included in the analysis) that correspond to the subfamily Mandageriinae (Young, 2008). The lack of marginal coronoid teeth can thus be treated as a probable apomorphy of the Mandageriinae.

On the other hand, in every taxa we surveyed (with the notable exception of rhizodontids, where no satisfying data on the palate is available; see Jeffery, 2012:table 1), marginal teeth rows were present on the palate bone, including *Cabonnichthys* and *Mandageria* (Ahlberg and Johanson, 1997:fig. 7). The clear lack of marginal teeth row in our specimen, supported by the CT-Scan data, allow us to conclude that it most probably corresponds to a lower jaw, instead of an upper jaw with associated palatal elements.

The dentition pattern observed on MNHN.F.URP 550, with the combination of a dentary fang and the lack of marginal teeth rows, can correspond to two taxa: rhizodontids and mandageriine tristichopterids.

**Probable systematic attribution –** According to the evidences herein presented, rhizodontids and mandageriine tristichopterids are the only candidate taxa for the systematic attribution of MNHN.F.URP 550, based on the lack of cosmine, polyplocodont-type plicidentine and the peculiar dentition pattern.

Rhizodontid lower jaws anatomy was reviewed by Jeffery (2002), based on *Rhizodus*. In this genus at least, mandibles are typically very narrow linguolabially and deep dorsoventrally, which is not the case in our specimen. *Rhizodus* also lacks pre- and intercoronoid fossae, while MNHN.F.URP 550 shows a probable intercoronoid fossa between the first and second coronoid (fig. 3, 4). Finally, rhizodontid fangs are noticeably curved posteriorly and lack cutting edges, contrary to tristichopterid fangs. Our specimen's teeth are straight (at least for the anterior coronoid fang) and flattened distally, which possibly correspond to a cutting edge.

All these observations, while less supported than the dentition pattern or the microanatomy, point towards an attribution of our specimen to the Tristichopteridae, and amongst them, to the Mandageriinae.

## CONCLUSION

The tristichopterids are a group of interest for Devonian vertebrate workers, because of their status of sister-group to the elpistostegalians (which include tetrapods) and their worldwide geographic distribution at the end of the Devonian. The specimen described herein

is a probable tristichopterid, possibly belonging to the subfamily Mandageriinae. Its description adds one Northern Gondwana occurrence to this clade, and expands the diversity of vertebrates known from the Devonian of Middle East.

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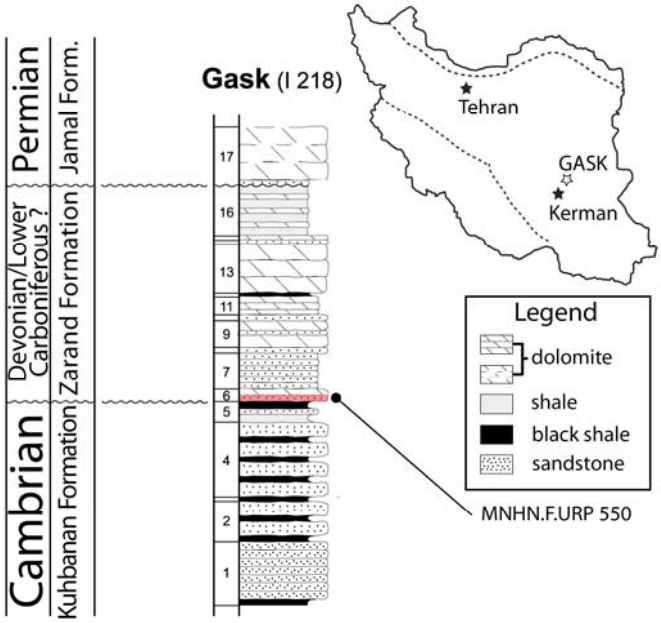
**FIGURE CAPTIONS**

**Figure 1**

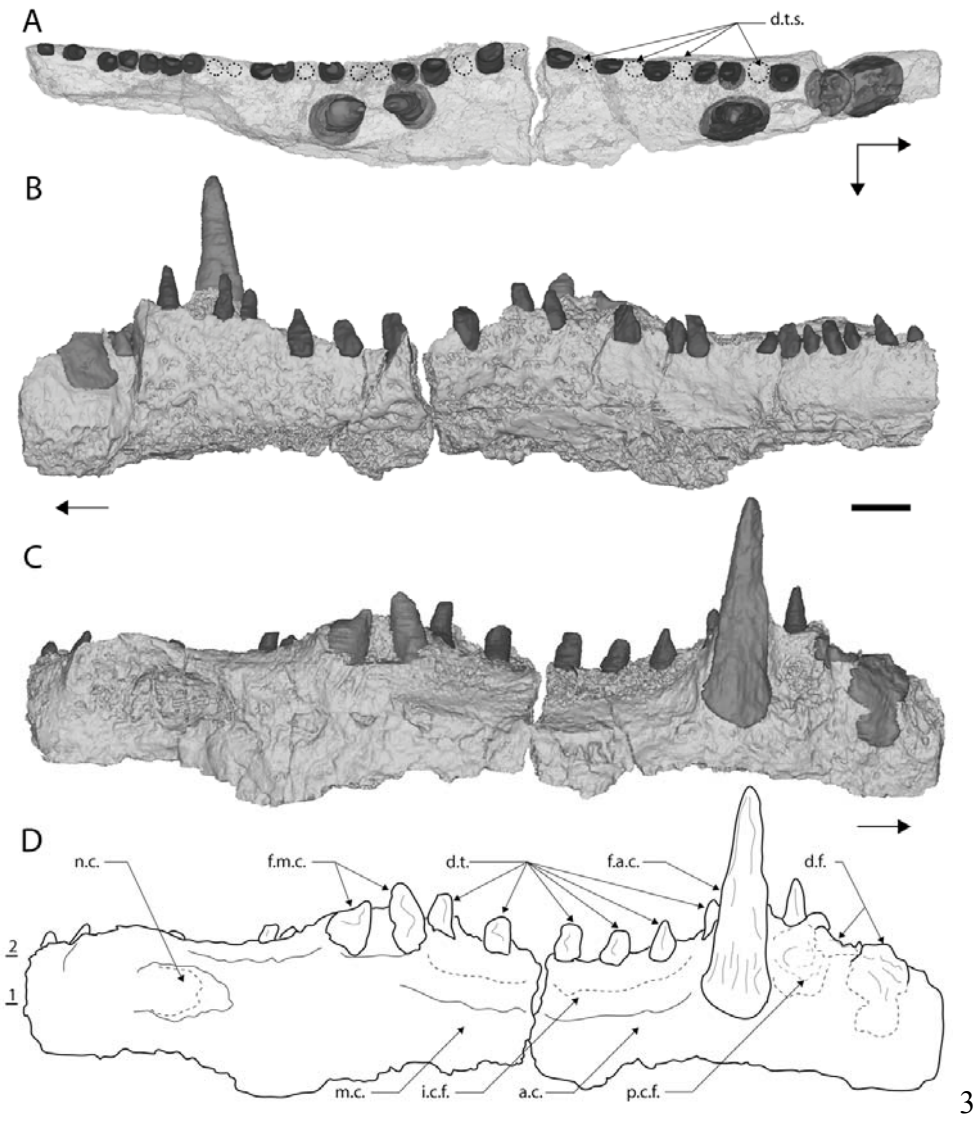



Location and stratigraphy of the Gask fossil site. Modified from Wendt et al., 2002. [Planned for column width]

**Figure 2**

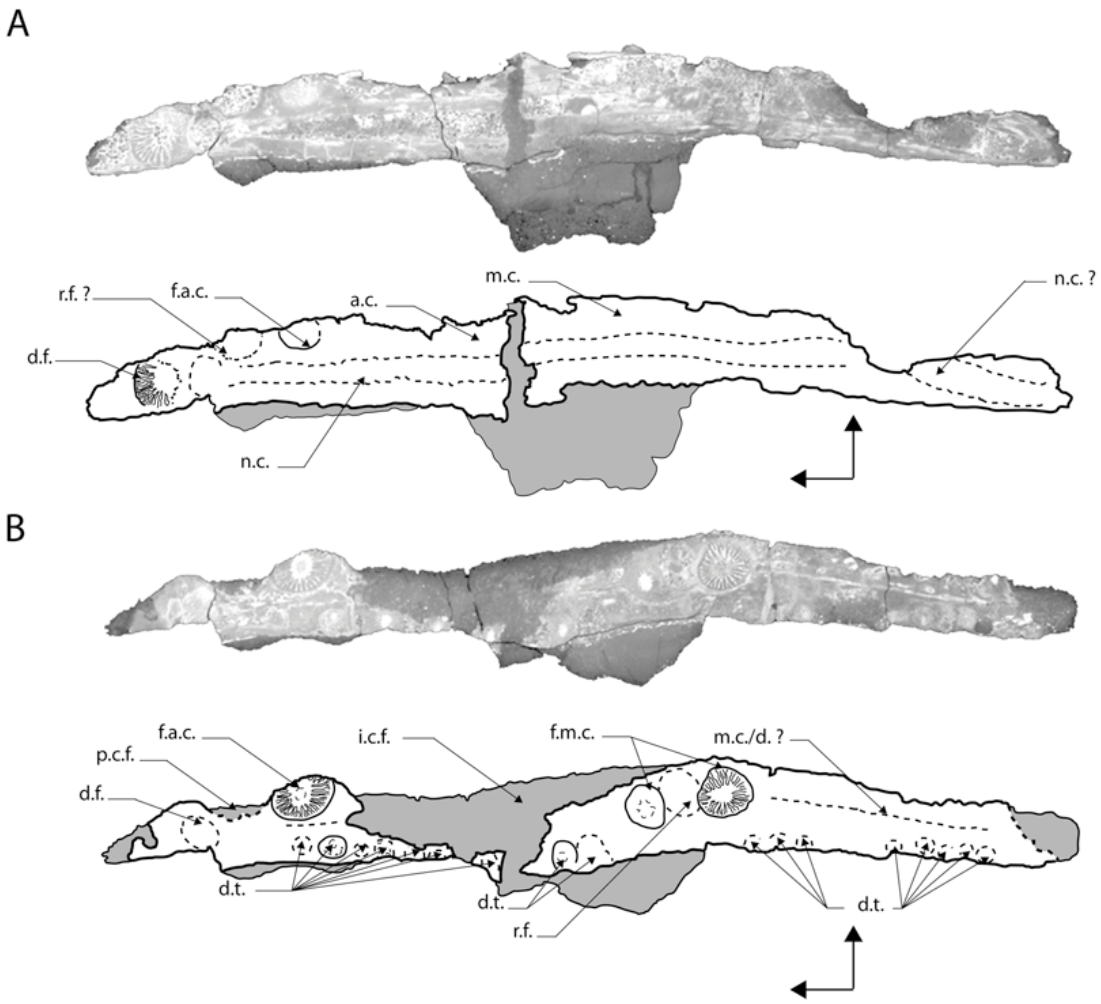
Tristichopteridae indet., MNHN.F.URP 550: photograph of the specimen in lingual view, embedded in the rock matrix. Scale bar equals 1 cm. Arrow points anteriorly. [Planned for page width]

**Figure 3**



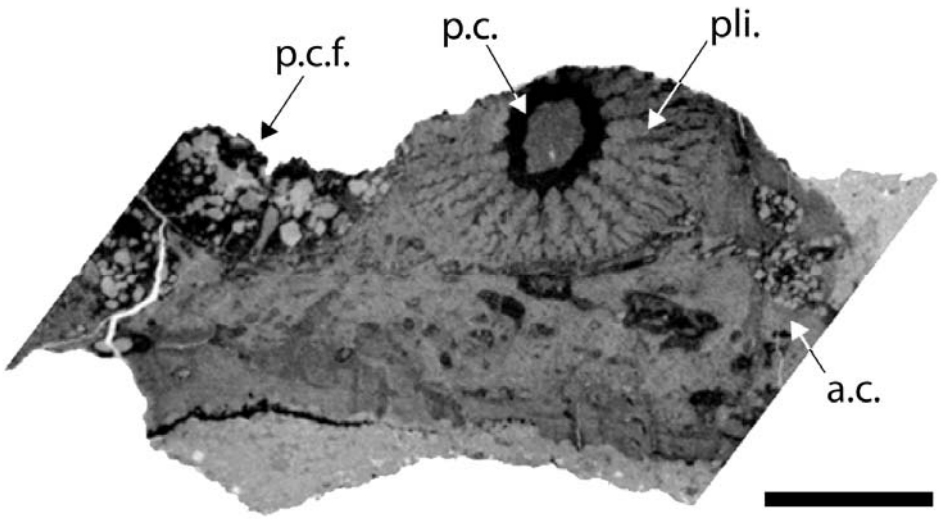

Tristichopteridae indet., MNHN.F.URP 550: 3D models of the left lower jaw, obtained with Mimics v.14.0. **A**: dorsal view; **B**: labial view; **C**: lingual view; **D**: interpretative drawing of the lingual view. Scale bar equals 1 cm. Arrows point to the anterior/lingual sides. Dashes 1 and 2 match respectively sections A and B of the Figure 4. **Abbreviations**: **a.c.**, anterior coronoid; **d.f.**, dentary fang; **d.t.**, dentary marginal teeth; **d.t.s.**, dentary marginal teeth sockets; **f.a.c.**, fang of the anterior coronoid; **f.m.c.**, fang pair of the middle coronoid; **i.c.f.**, anterior intercoronoid fossa; **m.c.**, middle coronoid; **n.c.**, nervous canal; **p.c.f.**, precoronoid fossa. [Planned for page width]

**Figure 4**




Tristichopteridae indet., MNHN.F.URP 550: virtual coronal sections of the left lower jaw. Scale bar equals 1 cm. Arrows point to the anterior/lingual sides. Note that section A is more ventral than section B (see Figure 3). **Abbreviations**: **a.c.**, anterior coronoid; **d.f.**, dentary fang; **d.t.**, dentary marginal teeth; **f.a.c.**, fang of the anterior coronoid; **f.m.c.**, fang of the middle coronoid; **i.c.f.**, anterior intercoronoid fossa; **m.c.**, middle coronoid; **m.c./d.**, middle coronoid/dentary junction; **n.c.**, nervous canal; **p.c.f.**, precoronoid fossa; **r.f.**, replacement fossa. [Planned for page width]

**Figure 5**




Tristichopteridae indet., MNHN.F.URP 550: virtual coronal section of the fang of the anterior coronoid (see Figures 2, 3, 4). The color pattern is inverted. Scale bar equals 5 mm. **Abbreviations**: **a.c.**, anterior coronoid; **p.c.**, pulp canal; **p.c.f.**, precoronoid fossa; **pli.**, plicidentine. [Planned for column width]

**Poster presented at the II International Obruchev Symposium on Palaeozoic Early Vertebrates, St Petersburg, Russia, August 2011.**

# Remains of a large non-tetrapod tetrapodomorph (Vertebrata, Sarcopterygii) from the Zarand Formation (Upper Devonian) of Southeastern Iran

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Here we report the study of an incomplete large jaw from the Devonian of Iran, initially attributed to a sarcopterygian indet. (Wendt *et al.* 2002). The specimen has been digitally studied by means of CT-Scan imaging, and 3D reconstruction.

## MATERIAL AND METHODS

The specimen studied here (fig.1) was collected by one of us (J.W.) during field works in Southeastern Iran in the end of the 1990's. It has been given to G.C. for study in 2006, and waits for an attribution in the MNHN collections.

The specimen comes from the Gask locality, near Kerman, Southeastern Iran (fig.2). Its stratigraphic position matches the Zarand Formation, considered Early Devonian to Early Carboniferous in age. Locally, there is an important discontinuity (a huge gap between the Cambrian Kuhbanan and the Devonian Zarand Formations), and the age of the fossil-yielding sediment is not precisely established. However, it has been assumed to be Late Devonian in age (Wendt *et al.* 2002). The paleo-environment is near-shore marine, possibly estuarine.

The bone-bearing matrix is a coarse sandstone conglomerate including large quartz pebbles (fig.1). The bone is incompletely visible, but looks fragile and highly microfracturated. Due to the heterogeneity of the surrounding matrix, it was impossible to prepare it using conventional, physical techniques.

Thus, it has been decided to study the specimen by CT-Scan imagery. Virtual extraction has been performed using the software Materialise© *Mimics* v. 14.0. Both the virtual sections and the 3D model obtained are highly informative (fig. 3, 4).

**Figure 1:** Studied specimen in its matrix. Scale bar = 1 cm. Photo: C. Lemzaouda/P. Loubry - MNHN.

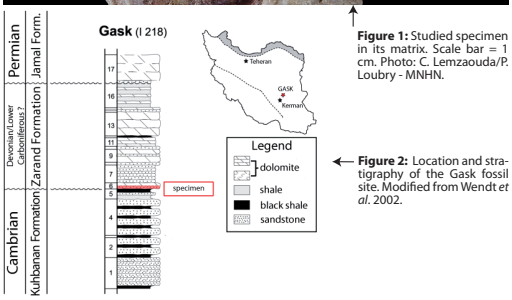


**Figure 2:** Location and stratigraphy of the Gask fossil site. Modified from Wendt *et al.* 2002.

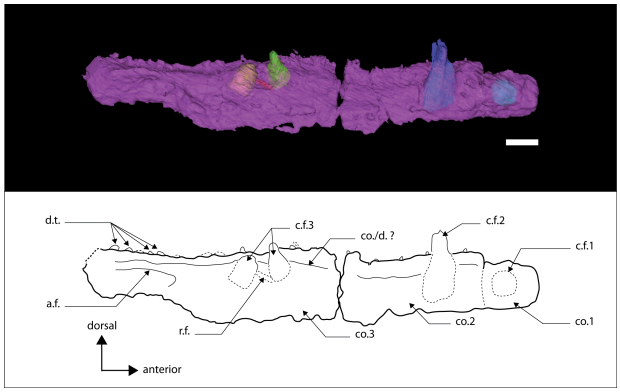


**Figure 3:** 3D model obtained with *Mimics* v.14.0 – left hemimandible in lingual view. Scale bar = 1 cm. Legend: c.f. = coronoid fangs ; co.1 = anterior coronoid ; co.2 = middle coronoid ; co.3 = posterior coronoid ; co./d. = coronoid/dentary junction ; d.t. = dentary marginal teeth ; a.f. = adductor fossa ; r.f. = replacement fossa.

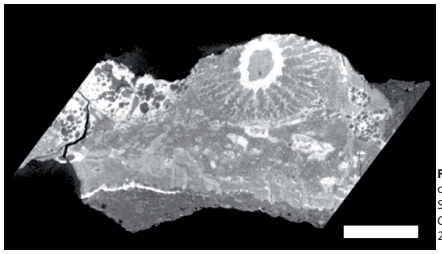

**Figure 4:** Virtual coronal section of the coronoid fang c.f.2. Scale bar = 5 mm. Credits: AST-RX platform (UMS 2700, CNRS/MNHN).

## RESULTS

The 3D model (fig. 3) suggests that the specimen is an incomplete left mandible (lower jaw). Both anterior and posterior extremities are missing, as well as the ventral margin of the infradentaries. The three coronoid bones are visible, each bearing large coronoid fangs.

The histology of one of these fangs (fig. 3, c.f.2) has been studied thanks to high-resolution CT-Scan imaging (fig.4). The dentine is folded (plicidentine), matching the "polyplocodont" pattern, as defined by Schultze (1969). This type of dentine is usually associated with "ichthyan" tetrapodomorph sarcopterygians (that is, all non-tetrapod taxa closer to tetrapods than to lungfishes). It corroborates the interpretation of Wendt *et al.* (2002), concerning the nature of the specimen.

The specimen is also characterized by an absence of cosmine (a characteristic hard tissue covering the scales and dermal bones of early sarcopterygians). The loss of cosmine and the elongation of the posterior coronoid bone (fig. 3, co.3) are derived characters, which occur in the (tristichopterids+("panderichthyids"+tetrapods)) clade (Ahlberg and Johanson 1998). The presence of coronoid fangs considerably larger than the marginal teeth of the dentary bone (fig. 3, d.t.), suggests that the jaw cannot belong to a tetrapod where the coronoid fangs, if present, are usually smaller than the dentary teeth (Ahlberg and Clack 1998).

In the light of these observations, the specimen is attributed either to a tristichopterid, or a "panderichthyid" tetrapodomorph.

## CONCLUSIONS AND PERSPECTIVES

The Kerman region of Iran is characterized by a rich fauna of Devonian marine vertebrates (Hairapetian *et al.* 2000). However, neither tristichopterid sarcopterygians (which probably originated from Laurussia and reached Gondwana during the Middle-Late Devonian) nor "panderichthyids" (which are spread in Laurussia) have been described in this region so far. Therefore, our results imply that this specimen is the closest relative to tetrapods known from the Devonian of Iran.

This discovery improves our knowledge of tetrapodomorph occurrences in the various faunal provinces of the Devonian times. It is possibly useful in the testing of biogeographical and paleogeographical hypotheses.

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## **APPENDIX II.** Abstracts

**Abstract of the Oral Communication presented at the 12th International Symposium on Early/Lower Vertebrates, Dallas (Texas, United States).**

**MONDEJAR-FERNANDEZ, J.** & CLEMENT, G. 2011. Squamation pattern in the Porolepiformes *Heimenia ensis* (Dipnomorpha, Sarcopterygii) from the Lower-Middle Devonian of Spitsbergen; pp. 38 *in* Johnson, G. (ed.), *Icthyolith Issues, Special publications*: *12th International Symposium on Early / Lower Vertebrates*, Dallas, Texas, United States, June 2011.

### SQUAMATION PATTERN IN THE POROLEPIFORMES *HEIMENIA ENSIS* (DIPNOMORPHA, SARCOPTERYGII) FROM THE LOWER-MIDDLE DEVONIAN OF SPITSBERGEN

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New material of the "porolepidid" *Heimenia ensis* Ørvig 1969 (Porolepiformes, Dipnomorpha, Sarcopterygii) sheds light on the evolution of scale morphology in sarcopterygian fishes. This material consists of an articulated nearly complete body and numerous isolated scales from the lower Middle Devonian (Emsian-Eifelian) of Spitsbergen (Verdalen Member of the Stjørdalen Formation, Wood Bay Group).

*Heimenia* shows a squamation pattern that could be described as "intermediate" between those of *Porolepis* and the more derived Porolepiformes (Holoptychiidae). The scales can be divided into three different morphological types: [1] thick and rhombic, [2] intermediate and [3] thin and rounded. The rounded scales are present in the anterior third of the body, intermediate scales are located in the middle third and rhombic scales are present in the posterior third. Small rhombic scales are also present throughout the ventral region. The transition from one type of scale to the other is progressive throughout the body and every type of scale bears traces of a cosmine-cover, regardless of its overall shape. Paleohistological study of these scales shows that the thickness of the cosmine layer tends to decrease in the intermediate and rounded scales. However, the relative thickness of the bony basal layer increases from the rhombic to rounded scales.

The unique squamation pattern in *Heimenia*, which exhibits a continuum between different scale morphologies, is informative of the evolutionary steps from thick/rhombic scales covered with cosmine to thin/rounded scales lacking cosmine in Porolepiformes. Such morphological and histological changes are known to have occurred by convergence among different groups of sarcopterygian fishes (i.e. lungfishes and "Osteolepiformes"). Morphofunctional and ecological implications of this squamation evolution will also be considered.

**Abstract of the Poster presented at the II International Obruchev Symposium on Palaeozoic Early Vertebrates, St. Petersburg (Russia)**

DAVESNE, D., **MONDEJAR-FERNANDEZ, J.**, HAIRAPETIAN, V., RÜCKLIN, M., WENDT, J. & CLEMENT, G. 2011. Remains of a large non-tetrapod tetrapodomorph (Vertebrata, Sarcopterygii) from the Zarand Formation (Upper Devonian) of Southeastern Iran; pp: 29-30 *in Abstracts of the II International Obruchev Symposium on Palaeozoic Early Vertebrates*, St Petersburg, Russia, August 2011.

## REMAINS OF A LARGE TETRAPODOMORPH FISH FROM THE ZARAND FORMATION (UPPER DEVONIAN) OF SOUTHEASTERN IRAN

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An incomplete jaw with large teeth was discovered by one of us (J. W.) during geological prospection near the village of Gask, southeastern Iran. This locality is part of the Zarand Formation, which spans from the lowest Devonian up to Tournaisian. The material consists of a single large jaw, presumably a left mandible. It is preserved in a siliciclastic conglomerate, consisting of coarse sandstone with large quartz pebbles. This heterogeneity made it difficult to envisage a physical preparation of the specimen. As a consequence, it was visualized with CT-scan imaging, and a three-dimensional model was produced using the software *Mimics*. The anterior and posterior parts of the jaw are missing and the specimen underwent a side flattening, due to diagenetic process. However, as demonstrated by the presence of large fangs on the internal face of the jaw and other anatomical features, this material can almost certainly be assigned to a tetrapodomorph, and probably to a tristichopterid fish. Devonian tetrapodomorph fish remains are very scarce in Iran and, if our determination is correct, it would be the first occurrence of tristichopterid fish in this part of the northern margin of Gondwana.

**Abstract of the Oral Communication presented at the 5th RIF (French Ichthyological Meeting), Paris (France)**

**MONDEJAR-FERNANDEZ, J.** 2012. Diversité, structure et évolution des rayons des nageoires des sarcoptérygiens [*Diversity, structure and evolution of fin rays in sarcopterygians*]; pp: 124 *in 5ème Rencontres de l'Ichtyologie en France*, Paris, France, March 2012.

## DIVERSITE, STRUCTURE ET EVOLUTION DES RAYONS DERMIQUES DES SARCOPTERYGIENS

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Chez les ostéichtyens (poissons osseux) le squelette dermique des nageoires est une des structures clés du succès et de la diversification du groupe depuis leur apparition il y a au moins 420 millions d'années. Les rayons dermiques des nageoires constituent des surfaces de contrôle flexibles et manœuvrables fondamentales pour la nage. Les différents types de rayons des nageoires des vertébrés sont rassemblés sous le nom de dermotriches. Parmi les dermotriches, se différentient les rayons osseux, comme les lépidotriches et les camptotriches (ces derniers, présents uniquement chez les dipneustes), et les rayons non minéralisés d'origine collagénique, comme les actinotriches (chez l'ensemble des ostéichtyens) et les cératotriches (chez les chondrichtyens).

Les ostéichtyens comprennent deux grands groupes, les actinoptérygiens (poissons à nageoires rayonnées) et les sarcoptérygiens (poissons à nageoires charnues). Chez les chondrichtyens (requins, raies et chimères) et d'autres gnathostomes basaux (notamment les placodermes†) les rayons des nageoires sont principalement fibreux à tous les stades ontogénétiques. Au contraire, chez les ostéichtyens les nageoires des larves sont soutenues par des actinotriches, tandis que dans les stades adultes les actinotriches sont remplacées par des lépidotriches osseux. Primitivement, ces lépidotriches sont composés d'os dermique recouvert de dentine et d'émail. Ces deux couches externes de dentine et d'émail ont tendance à disparaître au cours de l'histoire évolutive des ostéichtyens comme chez les néoptérygiens, les coelacanthes et les dipneustes, mais sont encore présentes chez certains actinoptérygiens basaux (e.g., « paléonisciformes†» et *Polypterus*) et chez de nombreux sarcoptérygiens dévoniens (e.g., porolépiformes† et « ostéolépidides†»).

Les sarcoptérygiens présentent une plus grande diversité de forme, structure et arrangement des lépidotriches que les actinoptérygiens. Cette diversité comprend des lépidotriches « classiques » (segmentés et bifurqués distalement), de longs lépidotriches non segmentés (chez les rhizodontes† et les tétrapodes dévoniens), et des lépidotriches modifiés (les camptotriches des dipneustes). Cette diversité morphologique chez les sarcoptérygiens peut s'expliquer par de subtiles modifications au niveau de 3 axes du développement des lépidotriches (proximo-distal, antéro-postérieur et contralatéral). Ces changements concernent

notamment le développement de la segmentation et des bifurcations des rayons, la position des rayons dans les nageoires, et le rapport entre lépidotriches et os radiaux. Une des principales tendances évolutives affectant les lépidotriches des sarcoptérygiens concerne la réduction progressive des rayons dermiques au détriment des os endochondraux dans les nageoires paires au cours du Dévonien (-410 à -360 millions d'années) jusqu'à la disparition complète de ces rayons chez les tétrapodes. Cependant les premiers tétrapodes comme *Ichthyostega* ou *Acanthostega* conservent encore une nageoire caudale bien développée soutenue par des lépidotriches non segmentés.

La nomenclature principale utilisée pour définir les différents morphotypes des rayons des nageoires des vertébrés sera présentée afin de décrire en détail la diversité des rayons chez les ostéichtyens, puis plus précisément chez les sarcoptérygiens. Une révision de la morphologie et du développement de ces rayons nous permettra de proposer un modèle évolutif et développemental de la formation et la diversification morphologique des lépidotriches. Ce modèle pourra être utilisé, par exemple, pour mieux comprendre l'énigmatique maintien puis la perte des rayons chez les premiers tétrapodes.

**Mots clés** : actinotriches, camptotriches, évolution, lépidotriches, sarcoptérygiens

**APPENDIX III.** List of sarcopterygian species

The following list of sarcopterygian species was compiled during the course of my thesis to account for the taxonomical diversity of sarcopterygian fishes. The list includes all taxa assigned to the Sarcopterygii and stretches from the stem osteichthyans to the Devonian tetrapods. The Actinistia and Dipnoi lineages are detailed until Recent.

It was not in my scope to present here an ultimate and definitive list of sarcopterygian genera and species, but to begin a large project of species gathering. I am aware that the following list is incomplete, but my aim is to improve and complete it in time.

A 'consensual' systematic position has been assigned to every taxon. The interrelationships of certain sarcopterygian groups (e.g., actinistians, dipnoans, "osteolepiformes") are far from resolved, and therefore the systematics herein presented might certainly change in the future.

The main divisions correspond to the orders described in the Introduction (Chapter I), despite the paraphyletic nature of some of them (e.g., "Osteolepiformes" and "Elpistostegalia"). Genera and species are listed alphabetically in every group and/or subgroup (e.g. order, suborder, family, subfamily). Taxa not belonging to any family or subfamily are uncertainly located at the stem of the following group. The authorship of the name is detailed, however the bibliographical reference will not necessarily be found in the bibliography. Star indicates the type species for a given genus comprising two or more species.

## **OSTEICHTHYES** HUXLEY, 1880

*Andreolepis* GROSS, 1968
*Andreolepis hedei* GROSS, 1968 *
*Andreolepis petri* MÄRSS, 2001

*Naxilepis* WANG &DONG 1989
*Naxilepis gracilis* WANG & DONG 1989

*Orvikuina* GROSS, 1953
*Orvikuina vardiaensis* GROSS, 1953

*Terenolepis* BURROW, 1995
*Terenolepis turnerae* BURROW, 1995

CLADE UNNAMED (after FRIEDMAN & BRAZEAU, 2010)

*Dialipina* SCHULTZE, 1968
*Dialipina salgueiroensis* SCHULTZE, 1968 *
*Dialipina markae* SCHULTZE, 1977

*Ligulalepis* SCHULTZE, 1968
*Ligulalepis yunnanensis* WANG &DONG 1989
*Ligulalepis toombsi* SCHULTZE, 1968 *

INCERTAE SEDIS *Lophosteus* PANDER, 1856
*Lophosteus superbus* PANDER, 1856

## **SARCOPTERYGII** ROMER, 1955

*Achoania* ZHU *et al.*, 2001
*Achoania jarvikii* ZHU *et al.*, 2001

*Guiyu* ZHU *et al.*, 2009
*Guiyu oneiros* ZHU *et al.*, 2009

*Langdenia* JANVIER & PHUONG, 1999
*Langdenia campylognatha* JANVIER & PHUONG, 1999

*Meemannia* ZHU *et al.*, 2006
*Meemannia eos* ZHU *et al.*, 2006

*Psarolepis* YU, 1998
*Psarolepis romeri* YU, 1998

**ONYCHODONTIDA** ANDREWS 1973

*Bukanodus* JOHANSON *et al.*, 2007
*Bukanodus jesseni* JOHANSON *et al.*, 2007

*Grossius* SCHULTZE, 1973
*Grossius aragonensis* SCHULTZE, 1973

*Lukeus* YOUNG & SCHULTZE, 2005
*Lukeus abudda* YOUNG & SCHULTZE, 2005

*Onychodus* NEWBERRY, 1857
*Onychodus dellei* GROSS, 1942
*Onychodus jaeckeli* GROSS, 1965
*Onychodus jandemarrai* ANDREWS *et al.*, 2006
*Onychodus obliquedentatus* JESSEN, 1967
*Onychodus ostrovenisis* HUENE, 1943
*Onychodus sigmoides* NEWBERRY, 1857 *

*Qingmenodus* LU & ZHU, 2010
*Qingmenodus yui* LU & ZHU, 2010

*Strunius* JESSEN, 1966
*Strunius rolandi* GROSS, 1956 *
*Strunius walteri* JESSEN, 1966

**ACTINISTIA** COPE, 1871

*Chagrinia* SCHAEFFER, 1962
*Chagrinia enodis* SCHAEFFER, 1962

*Eoactinistia* JOHANSON *et al.*, 2006
*Eoactinistia foreyi* JOHANSON *et al.*, 2006

*Gavinia* LONG, 1999
*Gavinia syntrips* LONG, 1999

*Shoshonia* FRIEDMAN *et al.*, 2007
*Shoshonia arctopteryx* FRIEDMAN *et al.*, 2007

*Styloichthys* ZHU & YU, 2002
*Styloichthys changae* ZHU & YU, 2002

**DIPLOCERCIDIFORMES** SCHULTZE, 2004

**DIPLOCERCIDOIDEI** BERG, 1937

FAMILY **MIGUASHAIIDAE** SCHULTZE, 1993

*Miguashaia* SCHULTZE, 1973
*Miguashaia bureaui* SCHULTZE, 1973 *
*Miguashaia grossii* FOREY *et al.*, 2000

FAMILY **DIPLOCERCIDAE** STENSIÖ, 1922

*Diplocercides* STENSIÖ, 1922
*Diplocercides davisi* MOY-THOMAS, 1937
*Diplocercides heiligenstockienses* JESSEN, 1966
*Diplocercides jaekeli* STENSIÖ, 1922
*Diplocercides kayseri* VON KOENEN, 1895 *

*Euporosteus* JAEKEL, 1927
*Euporosteus eifelianus* JAEKEL, 1927

*Nesides* STENSIÖ, 1937
*Nesides schmidti* STENSIÖ, 1937

INCERTAE SEDIS *Dictyonosteus* STENSIÖ, 1918
*Dictyonosteus arcticus* STENSIÖ, 1918

**HADRONECTOROIDEI** LUND & LUND, 1984

FAMILY "**HADRONECTORIDAE**" LUND & LUND, 1984

*Allenypterus* MELTON, 1969
*Allenypterus montanus* MELTON, 1969

*Hadronector* LUND & LUND, 1984
*Hadronector donbairdi* LUND & LUND, 1984

*Holopterygius* JESSEN, 1973
*Holopterygius nudus* JESSEN, 1973

*Lochmocercus* LUND & LUND, 1984
*Lochmocercus aciculodontus* LUND & LUND, 1984

*Polyosterhynchus* LUND & LUND, 1984
*Polyosterhynchus simplex* LUND & LUND, 1984

FAMILY "**RHABDODERMATIDAE**" BERG, 1958

*Caridosuctor* LUND & LUND, 1984
*Caridosuctor populosus* LUND & LUND, 1984

*Rhabdoderma* REIS, 1888
*Rhabdoderma aldingeri* MOY-THOMAS, 1937
*Rhabdoderma ardrossense* MOY-THOMAS, 1937
*Rhabdoderma elegans* NEWBERRY, 1856 *
*Rhabdoderma exiguum* EASTMAN, 1902
*Rhabdoderma huxleyi* TRAQUAIR, 1881
*Rhabdoderma tinglyense* DAVIS, 1884
*? Rhabdoderma madagascariensis* WOODWARD, 1910
*? Rhabdoderma newelli* HIBBARD, 1933

*Synaptotylus* ECHOLS, 1963
*Synaptotylus newelli* ECHOLS, 1963

FAMILY **SASSENIIDAE** FOREY, 1998

*Sassenia* STENSIÖ, 1921
*Sassenia groenlandica* FOREY, 1998
*Sassenia tuberculata* STENSIÖ, 1921 *
*? Sassenia guttata* STENSIÖ, 1921

*Spermatodus* COPE, 1894
*Spermatodus pustulosus* COPE, 1894

**COELACANTHIFORMES** BERG, 1940

**COELACANTHOIDEI** BERG, 1937

FAMILY **LAUGIIDAE** BERG, 1940

*Coccoderma* QUENSTEDT, 1858
*Coccoderma bavaricum* REIS, 1888
*Coccoderma gigas* REIS, 1888
*Coccoderma substriolatum* REIS, 1888
*Coccoderma suevicum* QUENSTEDT, 1858 *
*? Coccoderma harlemensis* WINLER, 1871

*Laugia* STENSIÖ, 1932
*Laugia groenlandica* STENSIÖ, 1932

INCERTAE SEDIS *Piveteauia* LEHMAN, 1952
*Piveteauia madagascariensis* LEHMAN, 1952

FAMILY **WHITEIIDAE** SCHULTZE, 1993

*Garnbergia* MARTIN & WENZ, 1984
*Garnbergia ommata* MARTIN & WENZ, 1984

*Whiteia* MOY-THOMAS, 1935
*Whiteia africanus* BROOM, 1905
*Whiteia nielseni* FOREY, 1998
*Whiteia tuberculata* MOY-THOMAS, 1935
*Whiteia woodwardi* MOY-THOMAS, 1935 *

FAMILY **COELACANTHIDAE** AGASSIZ, 1844

*Axelia* STENSIÖ, 1921
*Axelia elegans* STENSIÖ, 1921
*Axelia robusta* STENSIÖ, 1921*

*Coelacanthus* AGASSIZ, 1844
*Coelacanthus banffensis* LAMBE, 1916
*Coelacanthus gracilis* AGASSIZ, 1844
*Coelacanthus granulatus* AGASSIZ, 1844 *
*Coelacanthus lunzensis* TELLER, 1891
*Coelacanthus welleri* EASTMAN, 1908

*'Coelacanthus' lunzensis* REISZ, 1900

*Guizhoucoelacanthus* LIU *et al.*, 2006
*Guizhoucoelacanthus guanlingensis* LIU *et al.*, 2006

*Scleracanthus* STENSIÖ, 1921
*Scleracanthus asper* STENSIÖ, 1921

*Ticinepomis* RIEPPEL, 1980
*Ticinepomis peyeri* RIEPPEL, 1980

*Wimania* STENSIÖ, 1921
*Wimania sinuosa* STENSIÖ, 1921
*? Wimania multistriata* STENSIÖ, 1921

INCERTAE SEDIS *Graphiurichthys* WHITE & MOY-THOMAS, 1937
*Graphiurichthys callopterus* KNER, 1866

*Hainbergia* SCHWEIZER, 1966
*Hainbergia granulata* SCHWEIZER, 1966

*Moenkopia* SCHAEFFER & GREGORY, 1961
*Moenkopia wellesi* SCHAEFFER & GREGORY, 1961

*Mylacanthus* STENSIÖ, 1921
*Mylacanthus lobatus* STENSIÖ, 1921 *
*Mylacanthus spinosus* STENSIÖ, 1921

*Sinocoelacanthus* LIU, 1964
*Sinocoelacanthus fengshanensis* LIU, 1964

**LATIMEROIDEI** SCHULTZE, 1993

FAMILY **MAWSONIIDAE** SCHULTZE, 1993

*Alcoveria* BELTAN, 1972
*Alcoveria brevis* BELTAN, 1972

*Axelrodichthys* MAISEY, 1986
*Axelrodichthys araripensis* MAISEY, 1986

*Changxingia* WANG & LIU, 1981
*Changxingia aspratilis* WANG & LIU, 1981

*Chinlea* SCHAEFFER, 1967
*Chinlea sorenseni* SCHAEFFER, 1967

*Diplurus* NEWBERRY, 1878
*Diplurus longicaudatus* NEWBERRY, 1878 *
*Diplurus newarki* BRYANT, 1934

*Libys* MÜNSTER, 1842
*Libys polypterus* MÜNSTER, 1842 *
*Libys superbus* ZITTEL, 1887

*Mawsonia* WOODWARD, 1907
*Mawsonia gigas* WOODWARD, 1907 *
*Mawsonia lavocati* TABASTE, 1963
*Mawsonia libyca* WEILER, 1935
*Mawsonia tegamensis* WENZ, 1973
*Mawsonia ubangiana* CASIER, 1961

*Parnaibaia* YABUMOTO, 2008
*Parnaibaia maranhaoensis* YABUMOTO, 2008

*Trachymetopon* HENNIG, 1951
*Trachymetopon liassicum* HENNIG, 1951

*Youngichthys* WANG & LIU, 1981
*Youngichthys xinghuainsis* WANG & LIU, 1981

INCERTAE SEDIS *Heptanema* BELLOTI, 1857
*Heptanema paradoxum* BELLOTI, 1857

*Indocoelacanthus* JAIN, 1974
*Indocoelacanthus robustus* JAIN, 1974

*Lualabaea* SAINT-SEINE, 1955
*Lualabaea lerichei* SAINT-SEINE, 1955 *
*Lualabaea henryi* SAINT-SEINE, 1955

*Moenkopia* SCHAEFFER & GREGORY, 1961
*Moenkopia wellesi* SCHAEFFER & GREGORY, 1961

*Rhipis* SAINT-SEINE, 1950
*Rhipis moorseli* SAINT-SEINE, 1950 *
*Rhipis tuberculata* CASIER, 1965

FAMILY **LATIMERIIDAE** BERG, 1940

*Holophagus* EGERTON, 1861
*Holophagus gulo* EGERTON, 1861

*Latimeria* SMITH, 1939
*Latimeria chalumnae* SMITH, 1939 *
*Latimeria menadoensis* POUYAUD *et al.*, 1999

*Macropoma* AGASSIZ, 1844
*Macropoma lewesiensis* MANTELL, 1822 *
*Macropoma praecursor* WOODWARD, 1909
*Macropoma speciosum* REUSS, 1857
*Macropoma willemoesii* VETTER, 1881

*Swenzia* CLÉMENT, 2005
*Swenzia latimerae* CLÉMENT, 2005

*Undina* MÜNSTER, 1834
*Undina cirinensis* THIOLLIÈRE, 1854
*Undina grandis* EASTMAN, 1914

*Undina penicillata* MÜNSTER, 1834 *
*Undina purbeckensis* WOODWARD, 1916
*? Undina barroviensis* WOODWARD, 1890
*? Undina grandis* EASTMAN, 1914
*? Undina picena* COSTA, 1862

INCERTAE SEDIS *Macropomoides* WOODWARD, 1942
*Macropomoides orientalis* WOODWARD, 1942

*Megalocoelacanthus* SCHWIMMER *et al.*, 1994
*Megalocoelacanthus dobiei* SCHWIMMER *et al.*, 1994

## **RHIPIDISTIA** COPE, 1887 *sensu* CLOUTIER & AHLBERG, 1996

*Grenfellia* JOHANSON & RITCHIE, 2000
*Grenfellia meemannae* JOHANSON & RITCHIE, 2000

## **DIPNOMORPHA** AHLBERG, 1991

*Arquatichthys* LU & ZHU, 2008
*Arquatichthys porosus* LU & ZHU, 2008

*Youngolepis* CHANG & YU, 1981
*Youngolepis praecursor* CHANG & YU, 1981

FAMILY **POWICHTHYIDAE** JESSEN, 1980

*Powichthys* JESSEN, 1975
*Powichthys spitsbergensis* CLÉMENT & JANVIER, 2004
*Powichthys thorsteinssoni* JESSEN, 1975 *

### **POROLEPIFORMES** *sensu* BERG, 1937

FAMILY "**POROLEPIDIDAE**" BERG, 1940

*Porolepis* WOODWARD, 1891
*Porolepis brevis* JARVIK, 1942
*Porolepis elongata* JARVIK, 1942
*Porolepis hefteri* GROSS, 1936
*Porolepis kureikensis* VOROBYEVA, 1963
*Porolepis posnansiensis* KADE, 1858 *
*Porolepis rhenana* GROSS, 1937
*Porolepis siegenensis* GROSS, 1936
*Porolepis spitsbergensis* JARVIK, 1942
*Porolepis taymirica* VOROBYEVA, 1963
*Porolepis uralensis* OBRUCHEV, 1938

*Heimenia* ØRVIG, 1969
*Heimenia ensis* ØRVIG, 1969

FAMILY **HOLOPTYCHIIDAE** OWEN, 1860

*Duffichthys* AHLBERG, 1992
*Duffichthys mirabilis* AHLBERG, 1992

*Glyptolepis* MILLER EX AGASSIZ, 1841
*Glyptolepis baltica* GROSS, 1930
*Glyptolepis bendini* LOHEST, 1888
*Glyptolepis elegans* AGASSIZ, 1844
*Glyptolepis leptopterus* AGASSIZ, 1844 *
*Glyptolepis groenlandica* JARVIK, 1972
*Glyptolepis microlepidotus* AGASSIZ, 1844
*Glyptolepis orbis* VON EICHWALD, 1844
*Glyptolepis paucidens* TRAQUAIR, 1888
*Glyptolepis orbis* VON EICHWALD, 1844
*Glyptolepis quadrata* VON EICHWALD, 1844
*Glyptolepis radians* LOHEST, 1888
*Glyptolepis remota* OBRUCHEV, 1941
*? Glyptolepis dellei* GROSS, 1942

*Hamodus* OBRUCHEV, 1933
*Hamodus luktevitshi* OBRUCHEV, 1933

*Holoptychius* AGASSIZ, 1839
*Holoptychius flemingi* AGASSIZ, 1844
*Holoptychius giganteus* AGASSIZ, 1845
*Holoptychius halli* NEWBERRY, 1889
*Holoptychius ishora* JAECKEL, 1929
*Holoptychius jarviki* CLOUTIER, 1996
*Holoptychius nobilissimus* AGASSIZ, 1839 *
*Holoptychius radiatus* NEWBERRY, 1889
*Holoptychius scheii* KIAER, 1915
*Holoptychius taylori* NEWBERRY, 1889
*Holoptychius tuberculatus* NEWBERRY, 1889

*Laccognathus* GROSS, 1941
*Laccognathus embryi* DOWNS ET AL, 2011
*Laccognathus grossi* VOROBYEVA, 2006
*Laccognathus panderi* GROSS, 1941 *

*Nasogaluakus* SCHULTZE, 2000
*Nasogaluakus chorni* SCHULTZE, 2000

*Paraglyptolepis* VOROBYEVA, 1987
*Paraglyptolepis karkiensis* VOROBYEVA, 1987

*Pseudosauripterus* BALL *et al.*, 1961
*Pseudosauripterus anglicus* BALL *et al.*, 1961

*Quebecius* SCHULTZE, 1973
*Quebecius quebecensis* WHITEAVES, 1889 *
*Quebecius williamsi* SCHULTZE, 1973

*Ventalepis* SCHULTZE, 1980
*Ventalepis ketleriensis* SCHULTZE, 1980

**DIPNOI** MÜLLER, 1845

*Diabolepis* CHANG & YU, 1984
*Diabolepis speratus* CHANG & YU, 1984

*Adololopas* CAMPBELL & BARWICK, 1998
*Adololopas* CAMPBELL & BARWICK, 1998

*Jessenia* OTTO & BARDENHEUER, 1996
*Jessenia concentrica* OTTO & BARDENHEUER, 1996

*Orlovichthys* KRUPINA, 1980
*Orlovichthys limnatis* KRUPINA, 1980

*Stomiahykus* BERNACSEK, 1977
*Stomiahykus thlaodus* BERNACSEK, 1977

*Rhinodipterus* ØRVIG, 1961
*Rhinodipterus ulrichi* ØRVIG, 1961

**"DIPNORHYNCHOIDEI"** SCHULTZE, 1992

*Apatorynchus* FRIEDMAN & DAESCHLER, 2006
*Apatorynchus opistheretmus* FRIEDMAN & DAESCHLER, 2006

FAMILY **URANOLOPHIDAE** MILES, 1977

*Uranolophus* DENISON, 1968
*Uranolophus wyomingensis* DENISON, 1968

FAMILY **DIPNORHYNCHIDAE** BERG, 1940

*Dipnorhynchus* WESTOLL, 1949
*Dipnorhynchus cathlesae* CAMPBELL & BARWICK, 1999
*Dipnorhynchus kiandrensis* CAMPBELL & BARWICK, 1982
*Dipnorhynchus kurikae* CAMPBELL & BARWICK, 1985
*Dipnorhynchus sussmilchi* THOMSON & CAMPBELL, 1971 *

*Eoctenodus* HILLS, 1929
*Eoctenodus microsoma* HILLS, 1929

*Iranorhynchus* JANVIER & MARTIN, 1978
*Iranorhynchus* JANVIER & MARTIN, 1978

*Sunwapta* THOMSON, 1967
*Sunwapta grandiceps* THOMSON, 1967

*Westollrhynchus* SCHULTZE, 2001
*Westollrhynchus lehmanni* WESTOLL, 1949

FAMILY **SPEONESYDRIONIDAE** CAMPBELL & BARWICK, 1990

*Cathlorhynchus* CAMPBELL *et al.*, 2009
*Cathlorhynchus trismodipterus* CAMPBELL *et al.*, 2009

*Ichnomylax* LONG *et al.*, 1994
*Ichnomylax kurnai* LONG *et al.*, 1994 *
*Ichnomylax karatajae* REISZ *et al.*, 2004

*Osteoplax* MCCOY, 1848
*Osteoplax erosa* MCCOY, 1848

*Speonesydrion* CAMPBELL & BARWICK, 1983
*Speonesydrion lehmanni* WESTOLL, 1949
*Speonesydrion iani* CAMPBELL & BARWICK, 1983 *

FAMILY **FLEURANTIIDAE** BERG, 1940

*Barwickia* LONG, 1992
*Barwickia downunda* LONG, 1992

*Fleurantia* GRAHAM-SMITH & WESTOLL, 1937
*Fleurantia denticulata* GRAHAM-SMITH & WESTOLL, 1937

*Howidipterus* LONG, 1992
*Howidipterus donnae* LONG, 1992

*Jarvikia* LEHMAN, 1959
*Jarvikia arctica* LEHMAN, 1959

FAMILY **CHIRODIPTERIDAE** CAMPBELL & BARWICK, 1990

*Chirodipterus* MILES, 1977
*Chirodipterus australis* MILES, 1977 *
*Chirodipterus liangchengi* SONG & CHANG, 1991
*Chirodipterus paddyensis* MILES, 1977
*Chirodipterus potteri* KEMP, 2001
*Chirodipterus wildungensis* GROSS, 1980

*Gogodipterus* LONG, 1992
*Gogodipterus paddyensis* MILES, 1977

*Palaedaphus* GERVAIS, 1852
*Palaedaphus insignis* GERVAIS, 1852

*Pillararhynchus* CAMPBELL & BARWICK, 1990
*Pillararhynchus longi* CAMPBELL & BARWICK, 1990

**"DIPTEROIDEI"** NIKOLSKI, 1954

*Amadeodipterus* YOUNG & SCHULTZE, 2005
*Amadeodipterus kencampbelli* YOUNG & SCHULTZE, 2005

*Harajicadipterus* CLEMENT, 2009
*Harajicadipterus youngi* CLEMENT, 2009

*Pinnalongus* NEWMAN & BLAAUWEN, 2007
*Pinnalongus saxoni* NEWMAN & BLAAUWEN, 2007

*Tarachomylax* BARWICK *et al.*, 1995
*Tarachomylax oepiki* BARWICK *et al.*, 1995

**INCERTAE FAMILIAE** *Melanognathus* JARVIK, 1967
*Melanognathus canadensis* JARVIK, 1967

FAMILY **"STOMIAHYKIDAE"** BERNACSEK, 1977

*Stomiahykus* BERNACSEK, 1977
*Stomiahykus thlaodus* BERNACSEK, 1977

FAMILY **"DIPTERIDAE"** OWEN, 1846

*Dipterus* SEDGEWICK & MURCHINSON, 1928
*Dipterus valenciennesi* SEDGEWICK & MURCHINSON, 1928

*Orlovichthys* KRUPINA 1980
*Orlovichthys limnatis* KRUPINA 1980

*Sorbitorhynchus* WANG *et al.,* 1993
*Sorbitorhynchus deleaskitus* WANG *et al.,* 1993

FAMILY **HOLODONTIDAE** GORIZDRO-KULCZYKA, 1950

*Holodipterus* MILES, 1977
*Holodipterus elderae* PRIDMORE *et al.*, 1977
*Holodipterus gogoensis* MILES, 1977 *
*Holodipterus longi* CAMPBELL & BARWICK, 1991
*Holodipterus meemannae* PRIDMORE *et al.*, 1977

*Iowadipterus* SCHULTZE, 1992
*Iowadipterus halli* SCHULTZE, 1992

FAMILY **"RHYNCHODIPTERIDAE"** MOY-THOMAS, 1939

*Griphognathus* MILES, 1977
*Griphognathus minutidens* GROSS, 1956
*Griphognathus sculpta* SCHULTZE, 1969
*Griphognathus whitei* MILES, 1977 *

*Rhynchodipterus* SÄVE-SÖDERBERGH, 1937
*Rhynchodipterus elginensis* SÄVE-SÖDERBERGH, 1937

*Soederberghia* LEHMAN, 1959
*Soederberghia groenlandica* LEHMAN, 1959 *
*Soederberghia simpsoni* AHLBERG *et al*, 2001

FAMILY **PHANEROPLEURIDAE** HUXLEY, 1861

*Andreyevichthys* KRUPINA, 1987
*Andreyevichthys epitomus* KRUPINA, 1987

*Oervigia* LEHMAN, 1959
*Oervigia nordica* LEHMAN, 1959

*Orlovichthys* KRUPINA *et al.*, 2001
*Orlovichthys limnatis* KRUPINA *et al.*, 2001

*Phaneropleuron* WESTOLL, 1949
*Phaneropleuron andersoni* WESTOLL, 1949

*Pentlandia* TRAQUAIR, 1888
*Pentlandia macroptera* TRAQUAIR, 1888

*Scaumenacia* TRAQUAIR, 1893
*Scaumenacia curta* WHITEAVES, 1881

**"URONEMIDAE"** NIKOLSKI, 1954

FAMILY **URONEMIDAE** TRAQUAIR, 1890

*Uronemus* AGASSIZ, 1844
*Uronemus lobatus* AGASSIZ, 1844
*Uronemus splendes* (TRAQUAIR, 1881), WATSON & GILL, 1923

FAMILY **CONCHOPOMATIDAE** BERG, 1940

*Conchopoma* KNER, 1868
*Conchopoma arctatum* (COPE, 1877) SCHULTZE, 1975
*Conchopoma edesi* DENISON, 1969
*Conchopoma exanthematicum* (COPE, 1873) SCHULTZE, 1975
*Conchopoma gadiforme* KNER, 1868 *

*Straitonia* THOMSON, 1965
*Straitonia watersoni* THOMSON, 1965

INCERTAE SEDIS *Monongahela* LUND, 1970
*Monongahela dunkardensis* LUND, 1973
*Monongahela stenodonta*, LUND, 1970 *

**"CTENODONTOIDEI"** NIKOLSKI, 1954

FAMILY **CTENODONTIDAE** WOODWARD, 1891

*Ctenodus* AGASSIZ, 1838
*Ctenodus cristatus* AGASSIZ, 1838
*Ctenodus interruptus* NARKAS, 1869
*Ctenodus romeri* THOMSON, 1965
*Ctenodus tardus* FRITSCH, 1889

*Delatitia* SMITH-WOODWARD, 1906
*Delatitia breviceps* SMITH-WOODWARD, 1906

*Eoctenodus* HILLS, 1929
*Eoctenodus microsoma* HILLS, 1929

*SEDIS MUTABILIS* *Paraceratodus* LEHMAN *et al.*, 1959
*Paraceratodus germani* LEHMAN *et al.*, 1959

FAMILY **SAGENODONTIDAE** JAEKEL, 1911

*Aphelodus* KEMP, 1993
*Aphelodus anapes* KEMP, 1993

*Parasagenodus* VOROBYEVA, 1972
*Parasagenodus sibiricus* VOROBYEVA, 1972

*Sagenodus* OWEN, 1867
*Sagenodus barrandei* FRITSCH, 1888
*Sagenodus carlinvillensis* ROMER & SMITH, 1934
*Sagenodus copeanus* WILLISTON, 1900
*Sagenodus inaequalis* OWEN, 1867 *
*Sagenodus quinquecostatus* TRAQUAIR, 1883
*Sagenodus obliquus* WATSON & GILL, 1923
*Sagenodus ohiensis* COPE, 1874
*Sagenodus periprion* COPE, 1878
*Sagenodus pertennis* EASTMAN, 1903
*Sagenodus serratus* NEWBERRY, 1874

FAMILY **GNATHORHIZIDAE** MILES, 1977

*Beltanodus* SCHULTZE, 1981
*Beltanodus ambilobensis* SCHULTZE, 1981

*Gnathoriza* COPE, 1883
*Gnathorhiza bogdensis* MINIKH, 1977
*Gnathorhiza bothrotreta* BERMAN,1976
*Gnathorhiza dikeloda* OLSON, 1951
*Gnathorhiza lozovskii* MINIKH, 1977
*Gnathorhiza noblensis* OLSON & QALY, 1972
*Gnathorhiza otschevi* MINIKH, 1977
*Gnathorhiza pusilus* (COPE, 1877) CARLSON, 1968
*Gnathorhiza serrata* COPE, 1883 *

*Gnathorhiza tatarica* MINIKH, 1989
*Gnathorhiza triassica* MINIKH, 1977

*Megapleuron* GAUDRY, 1881
*Megapleuron rochei* GAUDRY, 1881 *
*Megapleuron zangerli* SCHULTZE, 1977

INCERTAE SEDIS *Proceratodus* ROMER & SMITH, 1934
*Proceratodus carlinvillensis* ROMER & SMITH, 1934
*Proceratodus favosus* COPE, 1884

**CERATODONTOIDEI** NIKOLSKI, 1954

FAMILY **ARGANODONTIDAE** MARTIN, 1979

*Arganodus* MARTIN, 1979
*Arganodus arganensis* MARTIN, 1979
*Arganodus atlantis* MARTIN, 1979
*Arganodus dorotheae* CASE, 1921 *
*Arganodus multicristatus* VOROBYEVA & MINIKH, 1968
*Arganodus tiguidiensis* TABASTE, 1963
*Arganodus* cf. *A. tiguidiensis* KEMP, 1991

*Ferganoceratodus* NESOV & KAZNYSHKIN, 1985
*Ferganoceratodus jurassicus* NESOV & KAZNYSHKIN, 1985 *
*Ferganoceratodus martini* CAVIN *et al.*, 2007

FAMILY **CERATODONTIDAE** GILL, 1873

*Ariguna* WADE, 1935
*Ariguna formosa* KEMP, 1994

*Ceratodus* AGASSIZ, 1838
*Ceratodus acutus* PRIEM, 1924
*Ceratodus africanus* HAUG, 1905
*Ceratodus americanus* KNIGHT, 1898
*Ceratodus arenaceus* QUENSTEDT, 1883
*Ceratodus arganensis* MARTIN, 1979
*Ceratodus avus* WOODWARD, 1806
*Ceratodus bovisrivi* LINCK, 1962
*Ceratodus bucobaensis* MINIKH, 1977
*Ceratodus capensis* WOODWARD, 1889
*Ceratodus carinatus* SCHAAL, 1984
*Ceratodus casieri* CAPETTA, 1972
*Ceratodus concinnus* PLIENINGER, 1844
*Ceratodus diutinus* KEMP, 1993
*Ceratodus donensis* VOROBYEVA & MINIKH, 1968
*Ceratodus dorotheae* CASE, 1921
*Ceratodus elegans* VOLLRATH, 1923
*Ceratodus facetidens* CHABAKOV, 1931
*Ceratodus felchi* KIRKLAND, 1987
*Ceratodus formosus* WADE, 1935
*Ceratodus frazieri* OSTROM, 1970

*Ceratodus guentheri* MARSH, 1878
*Ceratodus gustasoni* KIRKLAND, 1987
*Ceratodus heshanggoensis* CHENG, 1980
*Ceratodus hislopianus* OLDHAM, 1859
*Ceratodus hunterianus* OLDHAM, 1859
*Ceratodus humei* PRIEM, 1914
*Ceratodus iheringi* AMEGHINO, 1906
*Ceratodus jechartiensis* MINIKH, 1977
*Ceratodus kannemeyeri* SEELEY, 1897
*Ceratodus kaupi* AGASSIZ, 1838 *
*Ceratodus latissimus* SCHMIDT, 1928
*Ceratodus madagascariensis* PRIEM, 1924
*Ceratodus madelungi* VOLZ, 1896
*Ceratodus multicristatus* VOROBYEVA & MINIKH, 1968
*Ceratodus minor* LIU & YEH, 1957
*Ceratodus minutus* HAUG, 1905
*Ceratodus nageshawarai* SHAH & SATSENGI, 1970
*Ceratodus nargun* KEMP, 1983
*Ceratodus orenburgensis* MINIKH, 1977
*Ceratodus palaeoruncinatus* FRENTZEN, 1924
*Ceratodus parvus* AGASSIZ, 1838
*Ceratodus pectinatus* TABASTE, 1963
*Ceratodus planasper* LINCK, 1962
*Ceratodus priscus* FRAAS, 1904
*Ceratodus robustus* KNIGHT, 1898
*Ceratodus shenmuensis* LIU & YEH, 1960
*Ceratodus sturi* TELLER, 1891
*Ceratodus szechuanensis* MARTIN & INGAVAT, 1982
*Ceratodus tuberculatus* TABASTE, 1963
*Ceratodus tiguidiensis* TABASTE, 1963
*Ceratodus wollastoni* CHAPMAN, 1914
*Ceratodus youngi* LIU & YEH, 1960
*Ceratodus yuanjiangensis* HUBEI, 1977
*? Ceratodus brasiliensis* SOUZA CUNHA & FERREIRA, 1980
*? Ceratodus ornatus* BROOM, 1909
*? Ceratodus recticristatus* VOROBYEVA & MINIKH, 1968

*Microceratodus* TEIXEIRA, 1954
*Microceratodus angolensis* TEIXEIRA, 1954

*Namatozodia* KEMP, 1993
*Namatozodia pitikanta* KEMP, 1993

*Ptychoceratodus* JAEKEL, 1926
*Ptychoceratodus donensis* VOROBYEVA & MINIKH, 1968
*Ptychoceratodus gracilis* VOROBYEVA & MINIKH 1968
*Ptychoceratodus philippsi* AGASSIZ, 1838
*Ptychoceratodus rectangulus* (LINCK, 1936) SCHULTZE, 1981
*Ptychoceratodus serratus (*AGASSIZ, 1838) SCHULTZE, 1981
*Ptychoceratodus wichmanni* APESTEGUIA *et al*., 2007

INCERTAE SEDIS *Metaceratodus* KEMP, 1991
*Metaceratodus palmeri* KEMP, 1991

*Gosfordia* WOODWARD, 1890
*Gosfordia truncata* WOODWARD, 1890

FAMILY **ASIATOCERATODONTIDAE** VOROBYEVA, 1967

*Asiaceratodus* VOROBYEVA, 1967
*Asiatoceratodus sharovi* VOROBYEVA, 1967

*Archaeoceratodus* KEMP, 1997
*Archaeoceratodus avus* WOODWARD, 1906
*Archaeoceratodus djelleh* KEMP, 1982
*Archaeoceratodus theganus* KEMP, 1997
*Archaeoceratodus rowleyi* KEMP, 1997

FAMILY **NEOCERATODONTIDAE** MILES, 1977

*Neoceratodus* CASTELNAU, 1876
*Neoceratodus denticulatus* HILLS, 1941
*Neoceratodus djelleh* KEMP, 1982
*Neoceratodus eyrensis* KEMP, 1982
*Neoceratodus forsteri* KREFFT, 1870 *
*Neoceratodus gregoryi* KEMP, 1982
*Neoceratodus tuberculatus* CHURCHER, 1995

*Mioceratodus* KEMP, 1992
*Mioceratodus anemosyrus* KEMP, 1992
*Mioceratodus diaphorus* KEMP, 1997
*Mioceratodus gregoryi* WHITE,1925 *
*Mioceratodus poastrus* KEMP, 1997

FAMILY **LEPIDOSIRENIDAE** BONAPARTE, 1841

*Lepidosiren* FITZINGER, 1837
*Lepidosiren paradoxa* FITZINGER, 1837

*Protopterus* OWEN, 1839
*Protopterus aethiopicus* STROMER, 1910
*Protopterus amphibius* STROMER, 1910
*Protopterus annectens* STROMER, 1910
*Protopterus protopteroides* MARTIN, 1982
*Protopterus libycus* STROMER, 1910

## **TETRAPODOMORPHA** AHLBERG, 1991

*Kenichthys* CHANG & ZHU, 1993
*Kenichthys campbelli* CHANG & ZHU, 1993

## **RHIZODONTIDA** ANDREWS & WESTOLL, 1970

*Archichthys* HANCOCK & ATHEY, 1870
*Archichthys portlocki* HANCOCK & ATHEY, 1870

*Barameda* LONG, 1989
*Barameda decipiens* LONG 1989 *
*Barameda mitchelli* HOLLAND *et al.*, 2007

*Gooloogongia* JOHANSON & AHLBERG, 1998
*Gooloogongia loomesi* JOHANSON & AHLBERG, 1998

*Letognathus* BRAZEAU, 2005
*Letognathus hardingi* (DAWSON, 1868) BRAZEAU, 2005

*Rhizodus* OWEN, 1840
*Rhizodus hibberti* OWEN, 1840

*Screbinodus* ANDREWS, 1985
*Screbinodus ornatus* TRAQUAIR, 1878

*Strepsodus* HUXLEY & ETHERIDGE 1865
*Strepsodus sauroides* BINNEY, 1841

INCERTAE SEDIS *Bogdanovia* OBRUCHEV, 1955
*Bogdanovia orientalis* OBRUCHEV, 1955

### FAMILY **SAURIPTERIDAE** DAVIS *et al.*, 2004

*Aztekia* JOHANSON & AHLBERG, 2001
*Aztekia mahalae* JOHANSON & AHLBERG, 2001

*Sauripterus* HALL, 1843
*Sauripterus taylori* HALL, 1843

## "**OSTEOLEPIFORMES**" JARVIK, 1942

### FAMILY "**OSTEOLEPIDIDAE**" COPE, 1889

*Gogonasus* LONG, 1985
*Gogonasus andrewsae* LONG, 1985

*Gyroptychius* MCCOY, 1848
*Gyroptychius agassizi* TRAILL, 1841 *
*Gyroptychius dolicotatus* JARVIK, 1985
*Gyroptychius elgae* VOROBYEVA, 1977

*Gyroptychius groenlandicus* JARVIK, 1950
*Gyroptychius grossi* VOROBYEVA, 1977
*Gyroptychius latvicus* VOROBYEVA, 1977
*Gyroptychius milleri* JARVIK, 1948
*Gyroptychius pauli* VOROBYEVA, 1977
*? Gyroptychius australis* YOUNG & GORTER, 1981
*? Gyroptychius kiaeri* JARVIK, 1949
*? Gyroptychius taylori* JESSEN, 1968

*Lamprotolepis* VOROBYEVA, 1977
*Lamprotolepis verrucosa* VOROBYEVA, 1977

*Latvius* JARVIK, 1948
*Latvius deckerti* JESSEN, 1973
*Latvius grewinky* GROSS, 1933 *
*Latvius niger* JESSEN, 1973
*Latvius obrutus* VOROBYEVA, 1977
*Latvius porosus* GREINER, 1977

*Litoptychus* DENISON, 1951
*Litoptychus bryanti* DENISON, 1951

*Medoevia* LEBEDEV, 1995
*Medoevia lata* LEBEDEV, 1995

*Megadonichthys* VOROBYEVA, 1962
*Megadonichthys kurikae* VOROBYEVA, 1962

*Muranjilepis* YOUNG & SCHULTZE, 2005
*Muranjilepis winterensis* YOUNG & SCHULTZE, 2005

*Osteolepis* AGASSIZ, 1835
*Osteolepis macrolepidotus* AGASSIZ, 1835 *
*Osteolepis panderi* JARVIK, 1948

*Owensia* HOLLAND, 2009
*Owensia chooi* HOLLAND, 2009

*Platyethmoidia* YOUNG *et al.*, 1992
*Platyethmoidia antartica* YOUNG *et al.*, 1992

*Thaumatolepis* OBRUCHEV, 1941
*Thaumatolepis edelsteini* OBRUCHEV, 1941

*Thursius* TRAQUAIR, 1888
*Thursius estonicus* VOROBYEVA, 1977
*Thursius macrolepidotus* SEDGWICK & MURCHINSON, 1829 *
*Thursius moy-thomasi* JARVIK, 1948
*Thursius pholidotus* TRAQUAIR, 1888
*Thursius talsiensis* VOROBYEVA, 1971
*Thursius wudingensis* FAN, 1992
*? Thursius fischeri* EICHWALD, 1860
*? Thursius minor* JARVIK, 1985

*Thysanolepis* VOROBYEVA, 1977
*Thysanolepis micans* VOROBYEVA, 1977

*Shirolepis* VOROBYEVA, 1977
*Shirolepis ananjevi* VOROBYEVA, 1977

*Sterropterygion* THOMSON, 1972
*Sterropterygion brandei* THOMSON, 1972

*Vorobjevaia* YOUNG *et al.*, 1992
*Vorobjevaia dolonodon* YOUNG *et al.*, 1992

*Yambira* JOHANSON & RITCHIE, 2000
*Yambira rhomsoni* JOHANSON & RITCHIE, 2000

INCERTAE SEDIS *Glyptopomus* AGASSIZ, 1844
*Glyptopomus minor* AGASSIZ, 1844*
*Glyptopomus elginensis* JARVIK, 1950
*Glyptopomus kinnairdi* HUXLEY, 1859
*Glyptopomus sayrei* NEWBERRY, 1878
*Glyptopomus ? bystrowi* GROSS, 1941

**MEGALICHTHYIFORMES** COATES & FRIEDMAN, 2010

FAMILY **MEGALICHTHYIDAE** HAY, 1902 (YOUNG *et al.*, 1992)

*Cladarosymblema* FOX *et al.*, 1995
*Cladarosymblema narrienense* FOX *et al.*, 1995

*Cryptolepis* VOROBYEVA, 1975
*Cryptolepis grossi* VOROBYEVA, 1975

*Ectosteorhachis* ROMER, 1937
*Ectosteorhachis nitidus* ROMER, 1937

*Lohsania* THOMSON & VAUGHN, 1968
*Lohsania utahensis* THOMSON & VAUGHN, 1968

*Mahalalepis* YOUNG *et al.*, 1992
*Mahalalepis resima* YOUNG *et al.*, 1992

*Megalichthys* AGASSIZ, 1835
*Megalichthys agassizianus* LOHEST, 1889
*Megalichthys coccolepis* YOUNG, 1870
*Megalichthys hibberti* AGASSIZ, 1843 *
*Megalichthys intermedius* WOODWARD, 1891
*Megalichthys laticeps* TRAQUAIR, 1884
*Megalichthys macropomus* COPE, 1880

*Megapomus* VOROBYEVA, 1977
*Megapomus heckeri* VOROBYEVA, 1977
*Megapomus markovskyi* VOROBYEVA, 1977
*Megapomus punctatus* VOROBYEVA, 1977

*Megistolepis* OBRUCHEV, 1955
*Megistolepis dorshkoji* VOROBYEVA, 1977
*Megistolepis klementzi* OBRUCHEV, 1955 *

*Palatinichthys* WITZMANN & SCHOCH, 2012
*Palatinichthys laticeps* WITZMANN & SCHOCH, 2012

*Sengoerichthys* JANVIER *et al.*, 2007
*Sengoerichthys ottoman* JANVIER *et al.*, 2007

FAMILY **CANOWINDRIDAE** YOUNG *et al.*, 1992

*Beelarongia* LONG, 1987
*Beelarongia patrichae* LONG, 1987

*Canowindra* THOMPSON, 1973
*Canowindra grossi* THOMPSON, 1973

*Howichthys* LONG & HOLLAND, 2008
*Howichthys warrenae* LONG & HOLLAND, 2008

*Koharalepis* YOUNG *et al.*, 1992
*Koharalepis jarviki* YOUNG *et al.*, 1992

FAMILY **RHIZODOPSIDAE** BERG, 1940

*Callistiopterus* ROMER, 1942
*Callistiopterus clappi* ROMER, 1942

*Marsdenichthys* LONG, 1985
*Marsdenichthys longioccipus* LONG, 1985

*Rhizodopsis* SCHULTZE & HEIDTKE, 1993
*Rhizodopsis hanbuchi* SCHULTZE & HEIDTKE, 1993
*Rhizodopsis sauroides* WILLIAMSON, 1837 *

*Taeniolepis* CHABAKOV, 1927
*Taeniolepis trautseholdi* CHABAKOV, 1927

**EOTETRAPODIFORMES** COATES & FRIEDMAN, 2010

FAMILY **TRISTICHOPTERIDAE** COPE, 1889

*Bruehnopteron* SCHULTZE & REED, 2012
*Bruehnopteron murphyi* SCHULTZE & REED, 2012

*Eusthenopteron* WHITEAVES, 1881
*Eusthenopteron farloviensis* WHITE, 1961
*Eusthenopteron foordi* WHITEAVES, 1881 *
*Eusthenopteron kurshi* ZUPINS, 2008
*Eusthenopteron obruchevi* VOROBYEVA, 1977

*Eusthenopteron saevesoederberghi* JARVIK, 1937
*Eusthenopteron traquairi* WESTOLL, 1937

*Heddleichthys* SNITTING, 2007
*Heddleichthys dalgleisiensis* ANDERSON, 1859

*Hyneria* THOMSON, 1968
*Hyneria lindae* THOMSON, 1968

*Jarvikina* ROHON, 1889
*Jarvikina wenjukowi* ROHON, 1889

*Langlieria* CLÉMENT *et al.*, 2009
*Langlieria socqueti* CLÉMENT *et al.*, 2009

*Tristichopterus* EGERTON, 1861
*Tristichopterus alatus* EGERTON, 1861

*Spodichthys* JARVIK, 1985
*Spodichthys buetleri* JARVIK, 1985

INCERTAE SEDIS *Platycephalichthys* VOROBYEVA, 1958
*Platycephalichthys bischoffi* VOROBYEVA, 1959 *
*Platycephalichthys rohoni* VOROBYEVA, 1962
*Platycephalichthys skuenicus* VOROBYEVA, 1962

*Tinirau* SWARTZ, 2012
*Tinirau clackae* SWARTZ, 2012

SUBFAMILY **MANDAGERIINAE** YOUNG, 2008

*Cabonnichthys* AHLBERG & JOHANSON, 1997
*Cabonnichthys burnsi* AHLBERG & JOHANSON, 1997

*Eusthenodon* JARVIK, 1952
*Eusthenodon gavini* JOHANSON & RITCHIE, 2000
*Eusthenodon waengsjoei* JARVIK, 1952 *

*Mandageria* JOHANSON & AHLBERG, 1997
*Mandageria fairfaxi* JOHANSON & AHLBERG, 1997

*Notorhizodon* YOUNG *et al.*, 1992
*Notorhizodon mackelveyi* YOUNG *et al.*, 1992

"**ELPISTOSTEGALIA**" CAMP & ALLISON, 1961
(**PANDERICHTHYIDA**) VOROBYEVA, 1989

*Elpistostege* WESTOLL, 1938
*Elpistostege watsoni* WESTOLL, 1938

*Panderichthys* GROSS, 1940
*Panderichthys rhombolepis* GROSS, 1940 *
*Panderichthys stolbovi* VOROBYEVA, 1980

*Tiktaalik* DAESCHLER *et al.*, 2006
*Tiktaalik roseae* DAESCHLER *et al.*, 2006

**TETRAPODA** HAWORTH, 1825 *sensu* GOODRICH, 1930

*Acanthostega* JARVIK, 1952
*Acanthostega gunnari* JARVIK, 1952

*Densignathus* DAESCHLER, 2000
*Densignathus rowei* DAESCHLER, 2000

*Elginerpeton* AHLBERG, 1998
*Elginerpeton pancheni* AHLBERG, 1998

*Hynerpeton* DAESCHLER *et al.*, 1994
*Hynerpeton bassetti* DAESCHLER *et al.*, 1994

*Ichthyostega* SÄVE-SÖDERBERGH, 1932
*Ichthyostega eigili* SÄVE-SÖDERBERGH, 1932
*Ichthyostega stensioei* SÄVE-SÖDERBERGH, 1932 *
*Ichthyostega watsoni* SÄVE-SÖDERBERGH, 1932

*Jakubsonia* LEBEDEV, 2004
*Jakubsonia livnensis* LEBEDEV, 2004

*Livoniana* AHLBERG *et al.*, 2000
*Livoniana multidentata* AHLBERG *et al.*, 2000

*Metaxygnathus* CAMPBELL & BELL, 1977
*Metaxygnathus denticulus* CAMPBELL & BELL, 1977

*Obruchevichthys* VOROBYEVA, 1977
*Obruchevichthys gracilis* VOROBYEVA, 1977

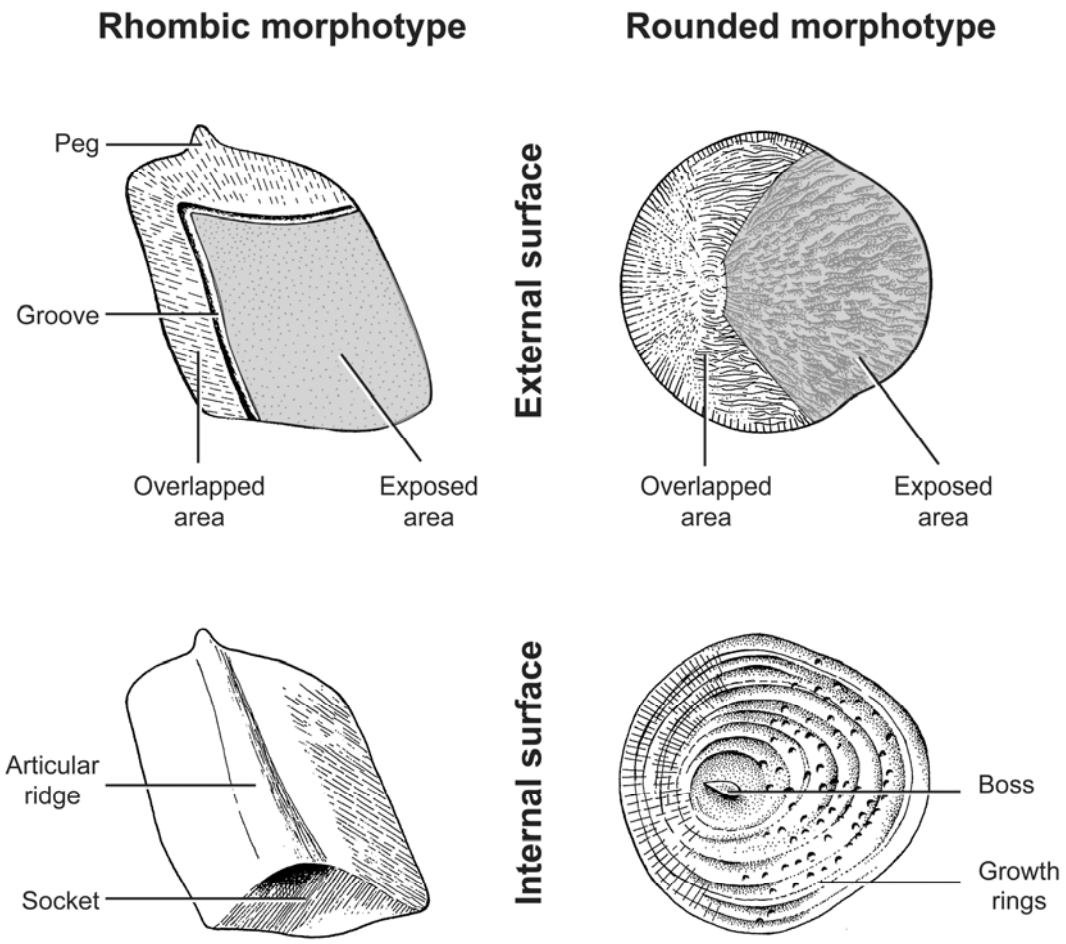
*Sinostega* ZHU *et al.*, 2002
*Sinostega pani* ZHU *et al.*, 2002

*Tulerpeton* LEBEDEV & COATES, 1995
*Tulerpeton curtum* LEBEDEV & COATES, 1995

*Ventastega* AHLBERG *et al.*, 1994
*Ventastega curonica* AHLBERG *et al.*, 1994

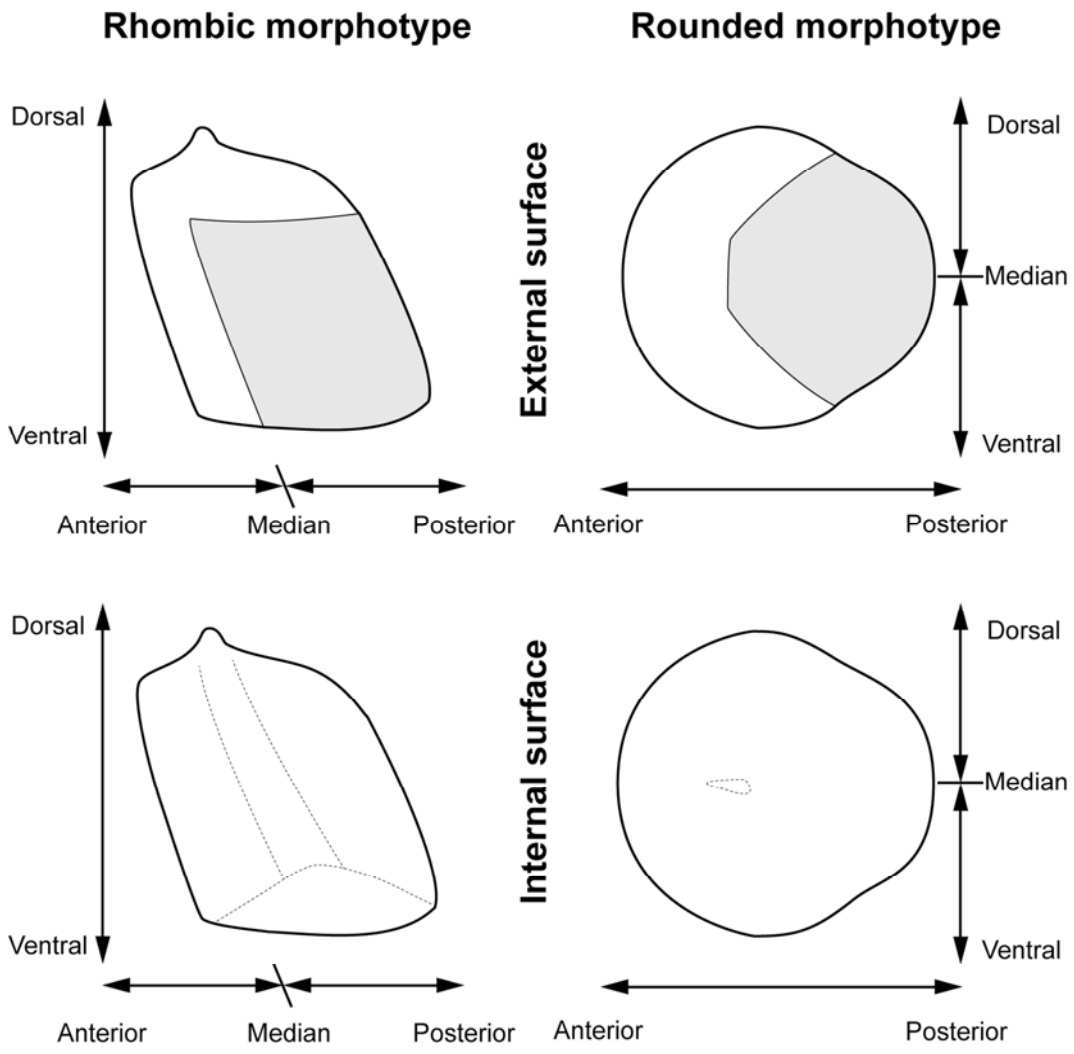
*Ymeria* CLACK *et al.*, 2012
*Ymeria denticulata* CLACK *et al.*, 2012

**APPENDIX IV.** Morphological references to the description of the scales




Modified after JARVIK, 1980a

**APPENDIX V.** Spatial references to the description of the scales




Modified after JARVIK, 1980a

**APPENDIX VI.** Scale table

The following table gives a broad overview of the shape, ornamentation and microstructure of the scales of sarcopterygians. It is based on a large number of bibliographical references and my personal observations on living and fossil scale specimens.

Logically, the list is mainly based on the taxa for which a certain amount of morphological and histological data was available. Therefore, some sarcopterygian fish genera and species are missing, but this is due to the lack of relevant information on their scales. It is thus implicit that further survey on these missing taxa is needed in order to complete the list. The taxa herein described were considered as representative of the different morphological and histological morphotypes.

| Systematics | | Geological occurrence | Scale external morphology | | | Scale microstructure | | | | | | | | | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | External morphology | | | | Histology | | | | | |
| | | | | | | | | Hard tissues ornamentation | | Superficial layer | | | | Basal layer | |
| | | | Overall shape | External surface | Internal surface | Overlapped area | Exposed area | Enamel | Dentine | Enamel | Dentine | Canal syst. (cosmine) | Spongiosa (vasc. layer) | Isopedine | Bone tissue (keel/boss) | |
| **Stem Sarcopterygii** | *Guiyu* | Late Silurian (China) | Rhombic | Extremely reduced, smooth anterior area; large sculptured posterior area | Flat to slightly concave, smooth, presence of an oblique articular ridge and a narrow 'socket' | Smooth, unornamented | Anostomosing ridges running parallel to the antero-posterior axis of the scale | Ganoine-like anostomosing ridges | | Presence of a ganoine-like tissue (single or multi-layered enamel) | Data not available | Data not available | Data not available | Data not available | Data not available | ZHU *et al.*, 2009, 2012 |
| | *Psarolepis* | Early Devonian (China) | | | | | Continuous covering of enamel layer; presence of pores in the enamel | Continuous layer of enamel covering the exposed area and overlying the dentine completely (cosmine-like tissue) | | Data not available | | | | | | CHEN, 2010 |
| | *Meemannia* | | Unknown | Data not available | Data not available | Data not available | Continuous covering of enamel layer; presence of pores in the enamel | Continuous layer of enamel covering the exposed area and overlying the dentine completely (cosmine-like tissue) | | Three or four superimposed layers of enamel (similar to ganoine) lining the upper part of the pore openings of the dentine | Numerous ramified dentinal tubules | Presence of a cosmine-like tissue, consisting of a network of horizontal and vertical canals in the dentine opening through pores in the enamel | Very thin (or absent) and vascularised made of pseudo-lamellar bone. Presence of numerous embedded odontodes | Thick, plywood structure of the collagen plies | Data not available | ZHU *et al.*, 2006, 2010 |
| **Onychodontida** | *Qingmenodus* | Early Devonian (China) | Unknown | Data not available | Data not available | Data not available | Continuous covering of enamel layer; presence of pores in the enamel | Continuous layer of enamel covering the exposed area and overlying the dentine completely (cosmine-like tissue) | | Data not available | Data not available | Presence of a cosmine-like tissue | Data not available | Data not available | Data not available | LU & ZHU, 2009 |
| | *Bukkanodus* | Early Devonian (Australia) | Rounded, with pointed posterior margin | Reduced, finely ridged anterior area; large sculptured posterior area | Concave and smooth with concentric growth lines | Radial ridges formed of closely packed spoon-shaped tubercles | Thick tubercles anteriorly, wide ridges separated by grooves containing pores posterioly | Dentine tubercles and ridges capped with a thin enamel layer | | | | Possible evidence of cosmine by the presence of pores in the exposed area | | | Absent | JOHANSON *et al.*, 2007 |
| | *Onychodus* | Middle Devonian (USA)<br>Late Devonian (Australia) | Rounded | Large, finely ridged, anterior area; reduced vermiculated posterior area | Flat and smooth, with concentric growth lines | Fine concentric rings formed by minute ridges, spoon-shaped tubercles posteriorly, near the edge with the exposed area | Spoon-shaped tubercles decreasing in size posteriorly, and sometimes fused to form radial ridges | Dentine tubercles capped with a thin enamel layer | | Thin, coating the tubercles and ridges | Few dentinal tubules | Absence of cosmine | Thin and densely vascularised made of pseudo-lamellar bone. Presence of embedded odontodes | Thick, plywood structure of the collagen plies | | ØRVIG, 1957; ANDREWS *et al.*, 2006 |
| | *Strunius* | Middle Devonian (Germany) | | | | Fine concentric rings formed by minute ridges | Spoon-shaped tubercles | | | Data not available | Data not available | | Data not available | Data not available | | JESSEN, 1966; pers. obs. |
| | *Grossius* | Middle Devonian (Spain) | Uncertain | Large anterior area; reduced unornamented posterior area | | Isolated, small spoon-shaped tubercles (certainly located near the edge with the exposed area) | Unornamented | Dentine tubercles of the overlapped area capped with a thin enamel layer | | | | | | | | SCHULTZE, 1973 |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Actinistia** | | *Styloichthys* | Early Devonian (China) | Rhombic | Extremely reduced, smooth anterior area; large sculptured posterior area | Flat to slightly concave, smooth, presence of an oblique articular ridge and a 'socket' | Smooth, separated from the exposed portion by a distinct groove; presence of an anterodorsal , lower anteroventral process and a dorsal 'peg' | Continuous covering of enamel layer; presence of pores in the enamel | Cosmine ridges obliquely arranged formed by depressions in the enamel | Data not available | Data not available | Presence of cosmine, histological structure unknown | Data not available | Data not available | Presence of an oblique articular ridge probably made of woven-fibered bone | LU & ZHU , 2008; ZHU *et al.*, 2010 |
| | Miguashaiidae | *Miguashaia* | Middle Devonian (Latvia)<br>Late Devonian (Québec) | Rounded | Large, finely striated anterior area; reduced, ridged posterior area | Flat to slightly concave and smooth, with concentric growth lines | Finely striated with radial ridges formed of closely packed spoon-shaped tubercles, and larger tubercles posteriorly, near the edge with the exposed area | Large spoon-shaped tubercles running into coarse ridges with fine chevron markings (highly variable depending on the position of the scales in the body) | Dentine tubercles and ridges capped with a thin enamel layer.<br>Continuous enamel covering of the posterior margin in certain scales | Thin, coating the tubercles, ridges, and the continuous posterior margin covering of certain scales | | Absence of cosmine, despite the presence of pores in the scales with continuous enamel covering | | | Absent | CLOUTIER, 1996; FOREY *et al.*, 2000 |
| | Diplocercidae | *Nesides* | Late Devonian (Germany) | | Large, unornamented anterior area; reduced, ridged posterior area | | Smooth or finely striated, spoon-shaped tubercles posteriorly, near the edge with the exposed area | Few elongate, separated ridges running parallel to the antero-posterior axis of the scale and converging posteriorly | Dentine tubercles and ridges capped with a thin enamel (or enameloid?) layer | Data not available | | Absence of cosmine | | | | STENSIÖ, 1937; FOREY, 1998 |
| | | *Diplocercides* | Late Devonian (Germany) | | | | | Few elongate, separated ridges running parallel to the antero-posterior axis of the scale | | | | | | | | STENSIÖ, 1937 |
| | "Rhabdodermathiidae" | *Rhabdoderma* | Carboniferous (U.K.) | | | | | Numerous elongate, separated ridges running parallel to the antero-posterior axis of the scale and converging posteriorly | | | | | | | | FOREY & YOUNG, 1985 |
| | Whiteiidae | *Whiteia* | Early Triassic (Madagascar) | | | | | Few elongate, separated ridges running parallel to the antero-posterior axis of the scale (in *W. woodwardi*) or isolated tubercles (in *W. tuberculata*) | | | | | | | | FOREY, 1998 |
| | ?Laughiidae | *Piveteauia* | Early Triassic (Madagascar) | | | | Smooth or finely striated | Few (fifteen), elongate, separated ridges running parallel to the antero-posterior axis of the scale | | | | | | | | CLÉMENT, 1999 |
| | Coelacanthidae | *Coelacanthus* | Late Triassic (USA) | | | | | Few (five) large, elongate, separated ridges running parallel to the antero-posterior axis of the scale | | | | | | | | SCHAEFFER, 1941 |
| | Latimeriidae | *Swenzia* | Late Jurassic (France) | | | | | Few (seven to nine), separated ridges running parallel to the antero-posterior axis of the scale | | | | | | | | CLÉMENT, 2005 |
| | | *Latimeria* | Extant (Indian Ocean) | | | | | Ornamented by a series of tubercles | Dentine tubercles capped with a thin enameloid layer | Thin enameloid coating the denticles | Numerous, richly branched dentinal tubes | | Thin and vascularised made of pseudo-lamellar bone. Presence of embedded odontodes | Irregularly mineralized isopedine with a twisted plywood-like structure of the collagen plies | | CASTANET *et al.*, 1975; MOYA-SMITH *et al.*, 1972; pers. obs. |

| | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **DIPNOMORPHA** | **Stem Dipnomorpha** | *Arquatichthys* | Early Devonian (China) | Rhombic | Reduced, smooth anterior area; large sculptured posterior area | Flat to slightly concave, smooth, presence of an oblique articular ridge and a broad 'socket' | Smooth, separated from the exposed portion by a distinct groove with three parallel striations anteriorly; presence of an anteroventral process and a dorsal 'peg' | Continuous covering of enamel layer; presence of pores in the enamel | Continuous layer of enamel covering the exposed area and overlying the dentine completely | | Data not available | Data not available | Presence of cosmine | Data not available | Data not available | Presence of an oblique articular ridge probably made of woven-fibered bone | LU & ZHU, 2008 |
| | | *Youngolepis* | | | | | Smooth, separated from the exposed portion by a distinct groove; presence of an anteroventral process and a dorsal 'peg' | | | | | | | | | LU & ZHU, 2008 |
| | | *Powichthys* | Early Devonian (Canada, Spitsbergen) | | | | | | | | | | | | | CLÉMENT & JANVIER, 2004 |
| | **Porolepiformes** | "Porolepididae" | *Porolepis* | Early Devonian (Germany, USA?) Middle Devonian (Spitsbergen, Baltic) | Rhombic | Reduced, smooth anterior area; large sculptured posterior area | Flat to slightly concave, smooth, presence of an oblique articular ridge and a narrow 'socket' | Smooth, separated from the exposed portion by a distinct groove; presence of a dorsal 'peg' | Continuous covering of enamel layer; presence of pores in the enamel; fine ridges anteriorly and dorsally developed | Continuous layer of enamel covering the exposed area | Small dentine tubercles in the anterior border of the cosmine, merging with the enamel layer posteriorly | Thin, lining the cosmine canals of the dentine | Numerous, richly branched dentinal tubes | Presence of cosmine, consisting of a network of horizontal and vertical canals in the dentine opening through pores in the enamel | Thin and densely vascularised made of pseudo-lamellar bone | Thick, made of ossified lamellar bone with a plywood-like structure of the collagen plies arranged orthogonally | Presence of an oblique articular ridge made of woven-fibered bone | ØRVIG, 1969b, pers. obs. |
| | | | *Heimenia* | Middle Devonian (Canada, Poland, Baltic, Belarus, Lithuania, Spitsbergen, Vietnam?, China?) | Rhombic, Rounded and Intermediate | | Flat to slightly concave, smooth, presence of an articular ridge and a narrow 'socket' (rhombic scales); reduction or absence of ridge, broadening of the 'socket' (intermediate and rounded scales) | Smooth, separated from the exposed portion by a distinct groove; presence of a dorsal 'peg' (in rhombic and intermediate scales), less marked groove anteriorly (in the rounded scales) | | | Thin, not lining the cosmine canals of the dentine | | | Thick and densely vascularised (rhombic scales), reduced (intermediate and rounded scales) made of pseudo-lamellar bone | Variable in thickness, made of ossified lamellar bone with a plywood-like structure of the collagen plies arranged orthogonally (rhombic) to twisted (intermediate and rounded) | Presence of an oblique articular ridge made of woven-fibered bone (rhombic), thinner and spreading over the internal surface (intermediate and rounded) | ØRVIG, 1969B, PAPER I |
| | | Holoptychiidae | *Glyptolepis* | Late Devonian (Greenland, Germany, Scotland) | Rounded | Reduced, smooth anterior area; large sculptured posterior area | Flat to slightly concave and smooth, with concentric growth lines | Smooth, presence of radiating rows of spoon-shaped tubercles near the edge with the exposed area | Large spoon-shaped tubercles running into thin ridges posteriorly | Dentine tubercles capped with a thin enamel layer | | Thin, coating the tubercles, although not uniformly present | Short, richly branching dentinal tubes in the tubercles and ridges | Absence of cosmine | Thick and densely vascularised made of pseudo-lamellar bone | Data not available | Absent | BYSTROW, 1939; ØRVIG, 1957 |
| | | | *Laccognathus* | Late Devonian (Arctic Canada, Russia, Latvia) | | | | | Blunt to spoon-shaped tubercles decreasing in size posteriorly | | | Thin, coating the tubercles | Short, richly branching dentinal tubes in the tubercles | | Thick and densely vascularised made of pseudo-lamellar bone. Presence of embedded odontodes | Thin, made of ossified lamellar bone with a plywood-like structure of the collagen plies arranged orthogonally | | ØRVIG, 1957, pers. obs. |
| | | | *Quebecius* | Late Devonian (Québec) | | | | Smooth, presence of small rounded tubercles near the edge with the exposed area | Large spoon-shaped tubercles running into thin ridges posteriorly, but not covering the entire surface of the scales | | | | Data not available | | Data not available | Data not available | | CLOUTIER & SCHULTZE, 1996 |
| | | | *Holoptychius* | Middle Devonian (Scotland, Baltic) Upper Devonian (Greenland, Scotland, Baltic, Russia, Siberia, Canada, USA, Colombia, Iran, Antarctica, Australia) | | Smooth anterior area; sculptured posterior area roughly equal en size | | Smooth, presence of radiating rows of spoon-shaped tubercles near the edge with the exposed area | Large and stout spoon-shaped tubercles running into coarse ridges posteriorly (the occurrence of ridges and tubercles is variable depending on the position of the scales in the body) | Absence of enamel | Tubercles and ridges solely made of dentine | Absence of enamel | Short, richly branching dentinal tubes in the tubercles and ridges | | Thick and densely vascularised made of pseudo-lamellar bone | Thick, made of ossified lamellar bone with a twisted plywood-like structure of the collagen plies | | ØRVIG, 1957, pers. obs. |

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| **DIPNOMORPHA** | | Dipnorhynchidae | *Dipnorhynchus* | Early – Middle Devonian (Australia) | Rhombic | Reduced, smooth anterior area; large sculptured posterior area | Flat to slightly concave, smooth, presence of an oblique articular ridge and a narrow 'socket' | Smooth, presence of a well-developed dorsal 'peg' | Continuous covering of enamel layer; presence of pores in the enamel; presence of small dentine tubercles in the anterior portion of the cosmine | Continuous layer of enamel covering the exposed area, presence of 'Westoll lines' | Small dentine tubercles in the anterior border of the cosmine, merging with the enamel layer posteriorly | Data not available | Data not available | Presence of cosmine, consisting of a network of horizontal and vertical canals in the dentine opening through pores in the enamel | Data not available | Data not available | Presence of an oblique articular ridge probably made of woven-fibered bone | THOMSON & CAMPBELL, 1971 |
| | | Uranolophidae | *Uranolophus* | Middle Devonian (USA) | | | | | | Continuous layer of enamel covering the exposed area | | Thin, capping the dentine | Numerous, branched dentinal tubes | | Thin and vascularised made of pseudo-lamellar bone. Presence of embedded odontodes | Thin, made of ossified lamellar bone with a plywood-like structure of the collagen plies arranged orthogonally | Presence of an oblique articular ridge made of woven-fibered bone | DENISON, 1969; CAMPBELL & BARWICK, 1988 |
| | **Dipnoi** | 'Dipteridae' | *Dipterus* | Late Devonian (Scotland, Germany) | Rounded | Large, smooth anterior area; reduced sculptured posterior area | Flat to slightly concave and smooth | Smooth, unornamented | Continuous covering of enamel layer; presence of pores in the enamel | Patches or continuous layer of enamel covering the exposed area | | Thin, sometimes lining the cosmine canals of the dentine | Numerous, branched dentinal tubes | Presence of cosmine, but irregularly developed | Thin and vascularised made of pseudo-lamellar bone. | Thin, made of ossified lamellar bone with a plywood-like structure of the collagen plies | Absent | GOODRICH, 1907; GROSS, 1956 |
| | | 'Rhynchodipteridae' | *Griphognathus* | Late Devonian (Germany, Australia) | | Large, unornamented anterior area; reduced, ridged posterior area | Flat to slightly concave and smooth | Finely striated with radiating rows of minute tubercles | Numerous fine, slightly undulating ridges, occupying the entire surface of the exposed area. certain scales covered by patches of cosmine | Absence of enamel and dentine (ridges solely made of bone) | | Absence of enamel, except in certain scales | Absence of dentine, except in certain scales | Cosmine patches present only in certain scales | Data not available | Data not available | | SCHULTZE, 1969 |
| | | Phaneropleuridae | Fleurantidae *Fleurantia* | Late Devonian (Canada) | | | Flat to slightly concave and smooth, with concentric growth lines | Smooth or finely striated with few well-delimited circuli | Numerous fine, slightly undulating ridges, occupying the entire surface of the exposed area (the number of ridges is variable depending on the position of the scales in the body) | Absence of enamel and dentine (ridges solely made of bone) | | Absence of enamel | Absence of dentine | Absence of cosmine | | | | ØRVIG, 1957; CLOUTIER, 1996 |
| | | | *Scaumenacia* | | | | | | | | | | | | | | | |
| | | | *Phaneropleuron* | Carboniferous (Scotland) | | | | | Numerous fine, slightly undulating ridges, occupying the entire surface of the exposed area | | | | | | Thick and densely vascularised made of pseudo-lamellar bone, presence of vertical canals opening through pores in the surface | Thin, made of ossified lamellar bone with a plywood-like structure of the collagen plies arranged orthogonally | | GOODRICH, 1907 |
| | | Neoceratodontidae | *Neoceratodus* | Extant (Australia) | | Large, ridged and spiny anterior area; reduced, ridged posterior area | Flat to slightly concave and smooth | Finely striated with presence of small spiny crests | Calcified polygonal plates ornamented by small spiny crests | Absence of enamel and dentine (calcified plates solely made of bone) | | | | | Thin, highly modified, forming the base of the calcified plates, presence of vertical canals opening between the spines through the surface | Thick, made of unmineralized lamellar bone with a plywood-like structure of the collagen plies arranged orthogonally | | BRIEN, 1958 |
| | | Lepidosirenidae | *Protopterus* | Extant (Africa) | | | | | | | | | | | | | | |
| | | | *Lepidosiren* | Extant (South America) | | | | | | | | | | | | | | |

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| **TETRAPODOMORPHA** | | | *Kenichthys* | Middle Devonian (China) | Rhombic | Reduced, smooth overlapped area; large sculptured exposed area separated by a groove | Flat to slightly concave, smooth, presence of an oblique articular ridge and a narrow 'socket' | Smooth, separated from the exposed portion by a distinct groove; presence of an reduced anteroventral process and a dorsal 'peg' | Continuous covering of enamel layer; presence of pores in the enamel | Continuous layer of enamel covering the exposed area and overlying the dentine completely | Data not available | Data not available | Presence of cosmine | Data not available | Data not available | Presence of a reduced articular ridge probably made of woven-fibered bone | CHANG & ZHU, 1995 |
| | **Rhizodontida** | | *Goologoongia* | Late Devonian (Australia) | Rounded | Large, unornamented anterior area; reduced, finely ridged posterior area triangular in shape | Flat to slightly concave with concentric growth lines and a central drop-shaped boss | Smooth, covered with radially arranged small denticles following the concentric growth lines | Numerous fine ridges occupying the entire surface of the exposed area, running parallel to the antero-posterior axis of the scale | Absence of enamel and dentine, ridges solely made of bone | Absence of enamel | Absence of dentine | Absence of cosmine | Data not available | Data not available | Presence of a small drop-shaped boss, certainly made of woven-fibered bone | JOHANSON & AHLBERG, 2001 |
| | | | *Sauripterus* | Late Devonian (USA) | | | | | | | | | | | | DAVIS *et al*., 2004 |
| | | | *Barameda* | Carboniferous (Australia) | | | | | | | | | | | | HOLLAND *et al*., 2007 |
| | | | *Strepsodus* | Carboniferous (Scotland) | | | | | | | | | | | | ANDREWS, 1985 |
| | **"Osteolepiformes"** | "Osteolepididae" | *Yambira* | Late Devonian (Australia) | Rhombic | Reduced, smooth overlapped area; large sculptured exposed area separated by a groove | Data not available | Smooth and unornamented | Ornamented with coarse bony tubercles | Absence of enamel and dentine, tubercles solely made of bone | Absence of enamel | Absence of dentine | Absence of cosmine | Data not available | Data not available | Data not available | JOHANSON & RITCHIE, 2000 |
| | | | *Medoevia* | Late Devonian (Russia) | Rhombic | Reduced, smooth overlapped area; large sculptured exposed area separated by a groove | Flat to slightly concave, smooth, presence of a 'vestigial' oblique articular ridge, absence of a marked 'socket' | Ornamented with fine ridges, separated from the exposed portion by a deep groove; absence of a well-developed dorsal 'peg' | Continuous covering of enamel layer; presence of pores in the enamel | Continuous layer of enamel covering the exposed area and overlying the dentine completely | Data not available | Data not available | Presence of cosmine | | | Presence of a reduced articular ridge probably made of woven-fibered bone | LEBEDEV, 1995 |
| | | | *Osteolepis* | Late Devonian (Scotland, Germany) | Rhombic | Reduced, smooth anterior area; large sculptured posterior area | Flat to slightly concave, smooth, presence of an oblique articular ridge and a narrow 'socket' | Smooth, separated from the exposed portion by a distinct groove; presence of a dorsal reduced "peg" | Continuous covering of enamel layer; presence of pores in the enamel | Continuous layer of enamel covering the exposed area | Thin, lining the cosmine canals of the dentine | Numerous, richly branched dentinal tubes | Presence of cosmine, consisting of a network of horizontal and vertical canals in the dentine opening through pores in the enamel | Thin and densely vascularised made of pseudo-lamellar bone | Thick, mado of ossified lamellar bone with a plywood-like structure of the collagen plies arranged orthogonally | Presence of an oblique articular ridge made of woven-fibered bone | GROSS, 1956, pers. obs. |
| | | | *Thursius* | | | | | | | Data not available | Data not available | Data not available | Presence of cosmine | Data not available | Data not available | | JARVIK, 1944,1985 |
| | | | *Latvius* | | | | | | | | | | | | | | |

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| **TETRAPODOMORPHA** | **"Osteolepiformes"** | Megalichthyidae | *Megalichthys* | Late Devonian - Carboniferous (Scotland, USA) | Rhombic | Reduced, smooth overlapped area; large sculptured exposed area separated by a deep groove | Flat to slightly concave, smooth, presence of an oblique articular ridge, presence of a broad 'socket' | Smooth, separated from the exposed portion by a deep groove; reduced dorsal 'peg' | Continuous covering of enamel layer; presence of pores in the enamel | Continuous layer of enamel covering the exposed area and overlying the dentine completely | Thin, not lining the cosmine canals of the dentine | Numerous, richly branched dentinal tubes | Presence of cosmine, consisting of a network of horizontal and vertical canals in the dentine opening through pores in the enamel | Thin and densely vascularised made of pseudo-lamellar bone | Thick, made of irregularly mineralized lamellar bone with a plywood-like structure of the collagen plies | Presence of an oblique articular ridge made of woven-fibered bone | GROSS, 1956; pers. obs. |
| | | | *Cladarosymblema* | Early Carboniferous (Australia) | | | Flat to slightly concave, smooth, presence of an oblique articular ridge, absence of a marked 'socket' | Smooth, separated from the exposed portion by a deep groove; absence of a dorsal 'peg' | | | | | | | | FOX *et al*., 1995 |
| | | | *Ectosteorhachis* | Early Permian (USA) | | | | | | Continuous layer of enamel or large blister of enamel and dentine overlying the spongiosa (in adult individuals) | | | | | | THOMSON, 1975 |
| | | Rhizodopsidae | *Rhizodopsis* | Carboniferous - Permian (Germany) | Rhomboid to Rounded | Large, unornamented anterior area; reduced, finely ridged posterior area | Flat to slightly concave with concentric growth lines and a central drop-shaped boss | Smooth, covered with minute concentric bony ridges | Numerous fine ridges occupying the entire surface of the exposed area intersected by larger concentric lines | Absence of enamel and dentine, ridges solely made of bone | Absence of enamel | Absence of dentine | Absence of cosmine | Data not available | Data not available | Presence of a small drop-shaped boss, probably made of woven-fibered bone | SCHULTZE & HEIDTKE, 1986 |
| | | | *Marsdenichthys* | Late Devonian (Australia) | | | | | | | | | | | | LONG, 1985; HOLLAND *et al*., 2010. |
| | | Canowindridae | *Koharalepis* | Middle-Late Devonian (Antarctica) | Rhombic | Reduced, smooth overlapped area; large sculptured exposed area separated by a groove | Flat to slightly concave, smooth, presence of an articular ridge, presence of a broad 'socket' | Smooth, separated from the exposed portion by a deep groove; presence of a dorsal 'peg' | Continuous covering of enamel layer; presence of pores in the enamel | Continuous layer of enamel covering the exposed area and overlying the dentine completely | Data not available | Data not available | Presence of cosmine | | | Presence of an oblique articular ridge probably made of woven-fibered bone | YOUNG *et al*., 1992 |
| | | | *Canowindra* | Late Devonian (Australia) | Rounded | Large, unornamented anterior area; reduced, finely ridged posterior area | Flat to slightly concave with concentric growth lines and a central drop-shaped boss | Smooth, covered with radial bony ridges | Numerous tubercles occupying the entire surface of the exposed area | Absence of enamel and dentine, tubercles solely made of bone | Absence of enamel | Absence of dentine | Absence of cosmine | | | Presence of a small drop-shaped boss, probably made of woven-fibered bone | THOMSON, 1973 |
| | | | *Beelarongia* | Early Carboniferous (Australia) | Rhombic | Reduced, smooth overlapped area; large sculptured exposed area separated by a groove | Flat to slightly concave, smooth, presence of an articular ridge, presence of a marked 'socket' | Smooth, separated from the exposed portion by a deep groove; presence of a well-developed dorsal 'peg' | Continuous covering of enamel layer; presence of pores in the enamel | Continuous layer of enamel covering the exposed area and overlying the dentine completely | Data not available | Data not available | Presence of cosmine | | | Presence of an oblique articular ridge probably made of woven-fibered bone | LONG, 1987 |

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| **TETRAPODOMORPHA** | **"Osteolepiformes"** | "Osteolepididae" | *Sterropterygion* | Late Devonian (USA) | Rhombic | Reduced, smooth overlapped area; large sculptured exposed area separated by a groove | Data not available | Smooth, separated from the exposed portion by a deep groove | Continuous covering of enamel layer; presence of pores in the enamel | Continuous layer of enamel covering the exposed area and overlying the dentine completely | Data not available | Data not available | Presence of cosmine | Data not available | Data not available | Data not available | THOMSON, 1972 |
| | | | *Litoptychus* | Late Devonian (USA) | Rounded | Large, unornamented anterior area; reduced, ornamented posterior area | Flat to slightly concave with concentric growth lines, absence of a central drop-shaped boss | Smooth, covered with minute concentric bony ridges | Numerous tubercles and ridges occupying the entire surface of the exposed area | Absence of enamel and dentine, Tubercles and ridges solely made of bone | Absence of enamel | Absence of dentine | Absence of cosmine | Thin and densely vascularised made of pseudo-lamellar bone | Thick, made of mineralized lamellar bone with a plywood-like structure of the collagen plies | Presence of a small drop-shaped boss, certainly made of woven-fibered bone | DENISON, 1951 |
| | | | *Gyroptychius* | Late Devonian (Scotland) | Rhombic | Reduced, smooth anterior area; large sculptured posterior area | Flat to slightly concave, smooth, presence of an oblique articular ridge and a narrow 'socket' | Smooth, separated from the exposed portion by a distinct groove; presence of a dorsal "peg" (rhombic and intermediate scales) | Continuous covering of enamel layer; presence of pores in the enamel; fine ridges anteriorly and dorsally developed | Continuous layer of enamel covering the exposed area | Data not available | Data not available | Presence of cosmine, consisting of a network of horizontal and vertical canals in the dentine opening through pores in the enamel | Thin and densely vascularised made of pseudo-lamellar bone | Thick, mado of ossified lamellar bone with a plywood-like structure of the collagen plies arranged orthogonally | Presence of an oblique articular ridge made of woven-fibered bone | JARVIK, 1985; pers. obs. |
| | | Tristichopteridae | *Spodichthys* | Late Devonian (Greenland) | Rounded | Large, unornamented anterior area; reduced, finely ridged posterior area | Flat to slightly concave with concentric growth lines and a central drop-shaped boss | Smooth, covered with radial bony ridges | Numerous small tubercles anteriorly and/or fine ridges occupying the entire surface of the exposed area, running parallel to the antero-posterior axis of the scale | Absence of enamel and dentine, ridges and tubercles solely made of bone | Absence of enamel | Absence of dentine | Absence of cosmine | Data not available | Data not available | Presence of a small drop-shaped boss, certainly made of woven-fibered bone | JARVIK, 1986; SNITTING, 2008 |
| | | | *Eusthenopteron* | Late Devonian (Québec, Baltic) | | | | | | | | | | Thin, formed by poorly-vascularized pseudo-lamellar bone, tubercles formed by a superficial layer of parallel-fibered bone above bundles of woven-fibered bone | Thick, made of mineralized lamellar bone with a twisted to orthogonal plywood-like structure of the collagen plies | | JARVIK, 1980; ZYLBERBERG *et al.*, 2010 |
| | | | *Eusthenodon* | Late Devonian (Canada, Greenland, Baltic, Belgium, Australia, South Africa) | | | | | Numerous ridges occupying the entire surface of the exposed area, running parallel to the antero-posterior axis of the scale | | | | | Data not available | Data not available | | CLÉMENT , 2002 |
| | | | *Notorhizodon* | Middle-Late Devonian (Antartica) | | | | Smooth, unornamented | | | | | | | | Data not available | YOUNG *et al.*, 1992 |
| | | | *Mandageria* | Late Devonian (Australia) | | | | | Broad undulating ridges separated by anteropotserior grooves occupying the entire surface of the exposed area, possible presence of small tubercles | | | | | | | | JOHANSON & AHLBERG, 1997 |
| | | | *Cabonnichthys* | | | | | | | | | | | | | | AHLBERG & JOHANSON, 1997 |

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| **TETRAPODOMORPHA** | **"Osteolepiformes"** | | *Glyptopomus* | Late Devonian (Scotland) | Rhombic | Reduced, smooth overlapped area; large sculptured exposed area separated by a groove | Flat to slightly concave, smooth, presence of an oblique articular ridge, presence of a broad 'socket' | Smooth, separated from the exposed portion by a groove; presence of a broad dorsal "peg | Ornamented with coarse bony tubercles | Absence of enamel and dentine, tubercles solely made of bone | Absence of enamel | Absence of dentine | Absence of cosmine | Data not available | Data not available | Data not available | JARVIK, 1950; PERS. OBS. |
| | **"Elpistostegalia"** | | *Elpistostege* | Late Devonian (Québec) | Rhombic | Reduced, smooth overlapped area; large sculptured exposed area separated by a groove | Flat to slightly concave, smooth, presence of an oblique articular ridge, presence of a broad 'socket' | Smooth, separated from the exposed portion by a groove; presence of a broad dorsal "peg | Ornamented with coarse bony tubercles | Absence of enamel and dentine, tubercles solely made of bone | Absence of enamel | Absence of dentine | Absence of cosmine | Data not available | Data not available | Data not available | SCHULTZE, 1996 |
| | | | *Panderichthys* | Late Devonian (Baltic, Russia) | | | | | | | | | | Thin, formed by richly vascularized pseudo-lamellar bone, tubercles formed by a superficial layer of parallel-fibered bone above bundles of woven-fibered bone | Thick, made of mineralized lamellar bone with an orthogonal plywood-like structure of the collagen plies | Presence of a small drop-shaped boss, certainly made of woven-fibered bone | WITZMANN, 2011 |
| | | | *Tiktaalik* | Late Devonian (Canada) | | | | | | | | | | | | | RICHTHER *et al.*, 2011 |
| | **Tetrapoda** | | *Acanthostega* | Late Devonian (Greenland) | Spindle-shaped to rounded | Homogenous and unornamented | Concave and deeply grooved mesailly | Smooth, unornamented | Smooth, unornamented | Absence of enamel and dentine, scales solely made of bone | Absence of enamel | Absence of dentine | Absence of cosmine | Data not available | Data not available | Data not available | COATES, 1996 |
| | | | *Ichthyostega* | | | | | | | | | | | | | | JARVIK, 1996 |
| | | | *Tulerpeton* | Late Devonian (Russia) | Ovoid to Rounded | Large, smooth overlapped area; Reduced, lightly sculptured exposed area | Concave, ornamented by small radial ridges made of beads of tubercles, presence of large concentric growth lines | Smooth, unornamented, presence of large concentric growth lines | Ornamented with small bony tubercles anteriorly | Absence of enamel and dentine, tubercles solely made of bone | Absence of enamel | Absence of dentine | Absence of cosmine | Avascular spongiosa made of dense parallel-fibered bone | Isopedine layer unknown (probably unmineralized) | Absence of the entire basal portion | LEBEDEV & COATES, 1995; Paper III |

## **APPENDIX VII.** List of institutional abbreviations

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| **ANSP** | Academy of Natural Sciences, Philadelphia, USA |
| **ESRF** | European Synchrotron Radiation Facility, Grenoble, France |
| **IVPP** | Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China |
| **GO** | Geologie und Paläontologie Institut der Universität Göttingen, Germany |
| **LIG** | Institute of Geology and Geography, Vilnius, Lithuania |
| **MB** | Museum für Naturkunde, Berlin, Germany |
| **MGUH** | Geological Museum of Copenhagen, Denmark |
| **MNHN** | Muséum National d'Histoire Naturelle, Paris, France |
| **NHM** | Natural History Museum, London, UK |
| **NMS** | National Museum of Scotland, Edinburgh, UK |
| **PIN** | Paleontological Institute of the Academy of Sciences of Russia, Moscow, Russia |
| **UAM** | Universidad Autónoma de Madrid, Spain |
| **UMA** | Universidad de Málaga, Spain |
| **UNDC** | Universidad Nacional de Colombia**,** Bogotá**,** Colombia |
| **UP** | University of Uppsala, Sweden |
| **UPMC** | Université Pierre et Marie Curie (Paris VI), Paris, France |
| **UV** | Universidad de Valencia, Spain |
| **SMNH** | Swedish Museum of Natural History, Stockholm, Sweden |

## **APPENDIX VIII.** Further data on the new developmental model

Any developmental process is composed in different stages at a morphological level. However, genetic studies further suggest that different molecular stages are also occurring. These genetic processes are organized in a hierarchical network initiated very early by the maternal genome. Transcriptional factors characterize the most important control by sequential regulation of downstream genes coding for further transcriptional factors in the network. Cell-to-cell or inter-tissue interactions further extend this network outside the cell regulating the transcriptions of all cells in a balanced way.

A secondary important aspect relates to cell or tissue differentiation. This process shows several morphological and physiological stages from an initial de-differentiation, where plurypotency of future cell fates occur, to further reversible commitment, reduction to multi or unipotency, irreversibility of commitment and morphological transformation finally. In these circunstancies, the concept positional information, or positional identity, are related to the activity of genes providing an information to cells dependent on their distance to organizing cells. Murciano (2003) and Marí-Beffa and Murciano (2010) have proposed that this initial process, which provide positional identity to cells, is a molecular mechanism distributed as a gradient along the proximodistal axis. A similar mechanism was proposed to regulate cell division during fin regeneration (Lee et al., 2005).

We use this simple positional model to explain our comparative data. Schematically, the model states the existence of a proximodistal gradient of positional identity (a molecular mechanism distributed in such a way) which generates differences along the axis. These differences are interpreted by cells to diferentiate along different pathways. The most important pathways associated with our study may be the actinotrichia forming cells pathway, the scleroblast pathway (lepidotrichia forming cells), the joint forming cell pathway or the ray bifurcation pathway. These pathways lead de-differentiated mesenchyme cells invading the fin fold to finally differentiate in actinotrichia, lepidotrichia or joint forming cells or to ectopically differentiate into interrays during ray branching. All these pathways could be under an upstream controlling mechanism distributed in a proximodistal gradient. As suggested from the comparatrive study, other process such as scale, internal cosmine and endoskeletal differentiation also to be downstream the same patterning mechanism. The potential complexity of the hierarchical network could thus be simplified into two processes: positional identity and its control of cell proliferation and cell differentiation.

How could a proximal differentiating tissue always substitute distally differentiating tissues? A possible mechanism may be based upon the concept of differentiation plasticity. Through a differentiation pathway many steps are necessary understood as a number of transcription factors to be synthetised in a sequential manner. If this is possible and a unique gradient mechanism controls the process we could consider that a preliminar common pathway exist for each cell type and that once a cell progress by repressing the possibility of the first cell type, i.e. actinotrichia forming cell pathway, the common pathway for a second differentiating option is openned, i.e. the lepidotrichia forming cell pathway. This sequential mechanism continues until the last endoskeleton pathway is activated and finished. A similar hierarchical network-like mechanism has been suggested for axis control in D. melanogaster, Xenopus laevis, zebrafish and many other model systems. Indeed, no developmental model system seems to be regulated in a different manner.

In our model, the gradient activates the flow along the pathway depending on its concentration/activation. Cell types that have been overactivated never flows back in a quasi-reversible way. These would account for the differentiation of the endoskeleton which appears after actinotrichia, the lepidotrichia which activates afterwards, the joint or the ossification pathways which are formed later and the ray bifurcation mechanism which would require much further control to be differentiated, probably dependent on other axes control.

During development, the gradient increases smoothly by constant activation in each cell. The form of the gradient may depend on distal conditions regulated by the distal organizer. If this is correct for a give position the transit along the differentiation pathways would depend on the continuous activation of the gradient. If a similar position haa more positional identity activation a next step in its differentiation may occur. This could explain some of the cell types already mentioned but some other could not be understood. This has led us to propose at least three different pathways regulated by the PI gradient.
Actinotrichia is first formed and its dissapearance during development let the endoskeleton to be sequentially formed. A first differentiation sequence could thus be the formation of actinotrichia in a first step and then endoskeletal formation in a second step. At low distal levels of the gradient actinotrichia could differentiate but at higher levels, in the same position, the endoskeleton is formed during the early stages of development.

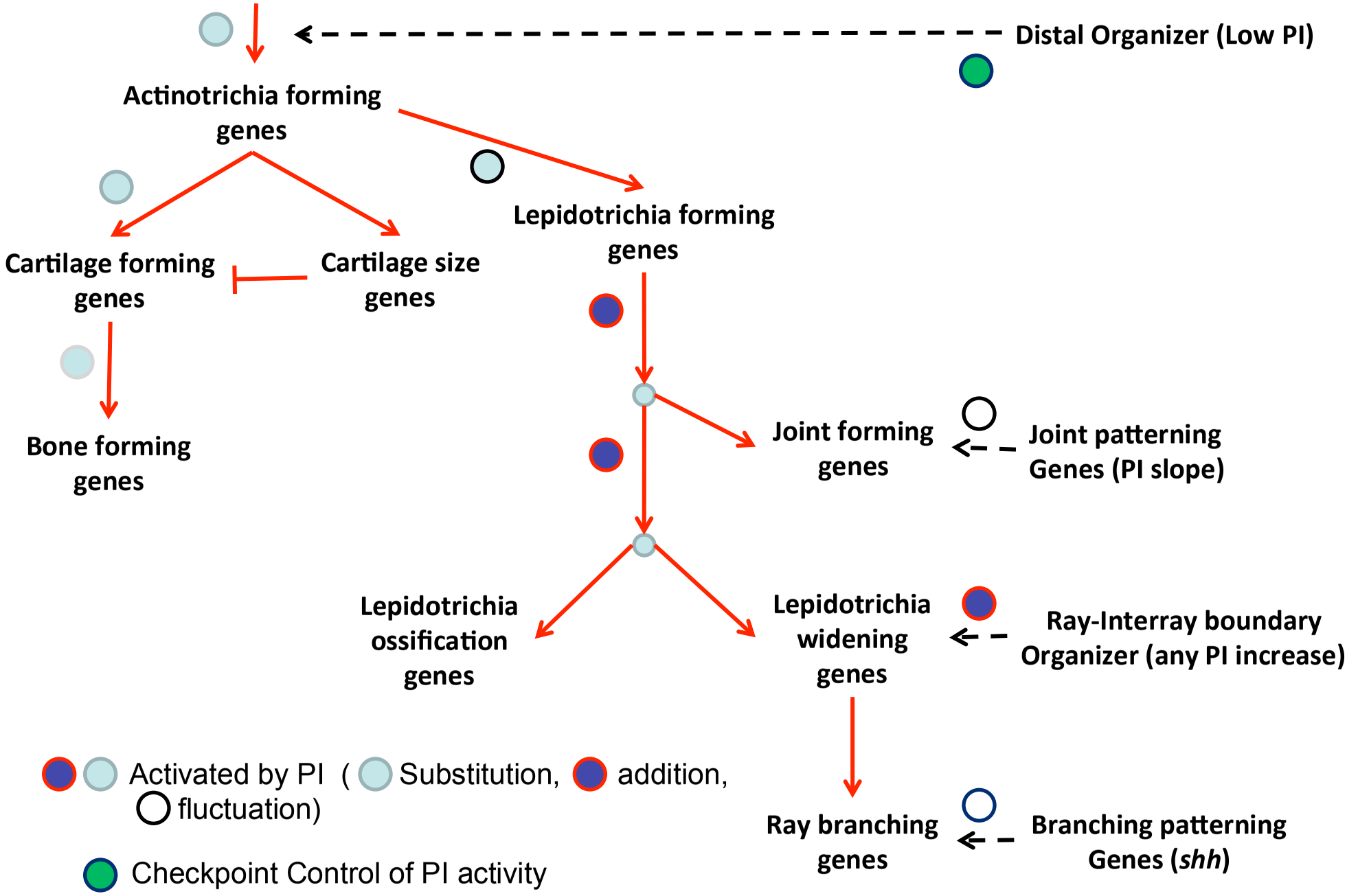
However, lepidotrichia appears later in an intercalary inbetween actinotrichia and endoskeleton. A simple mechanism, similar to those operating during Drosophila development, such as lateral inhibition,

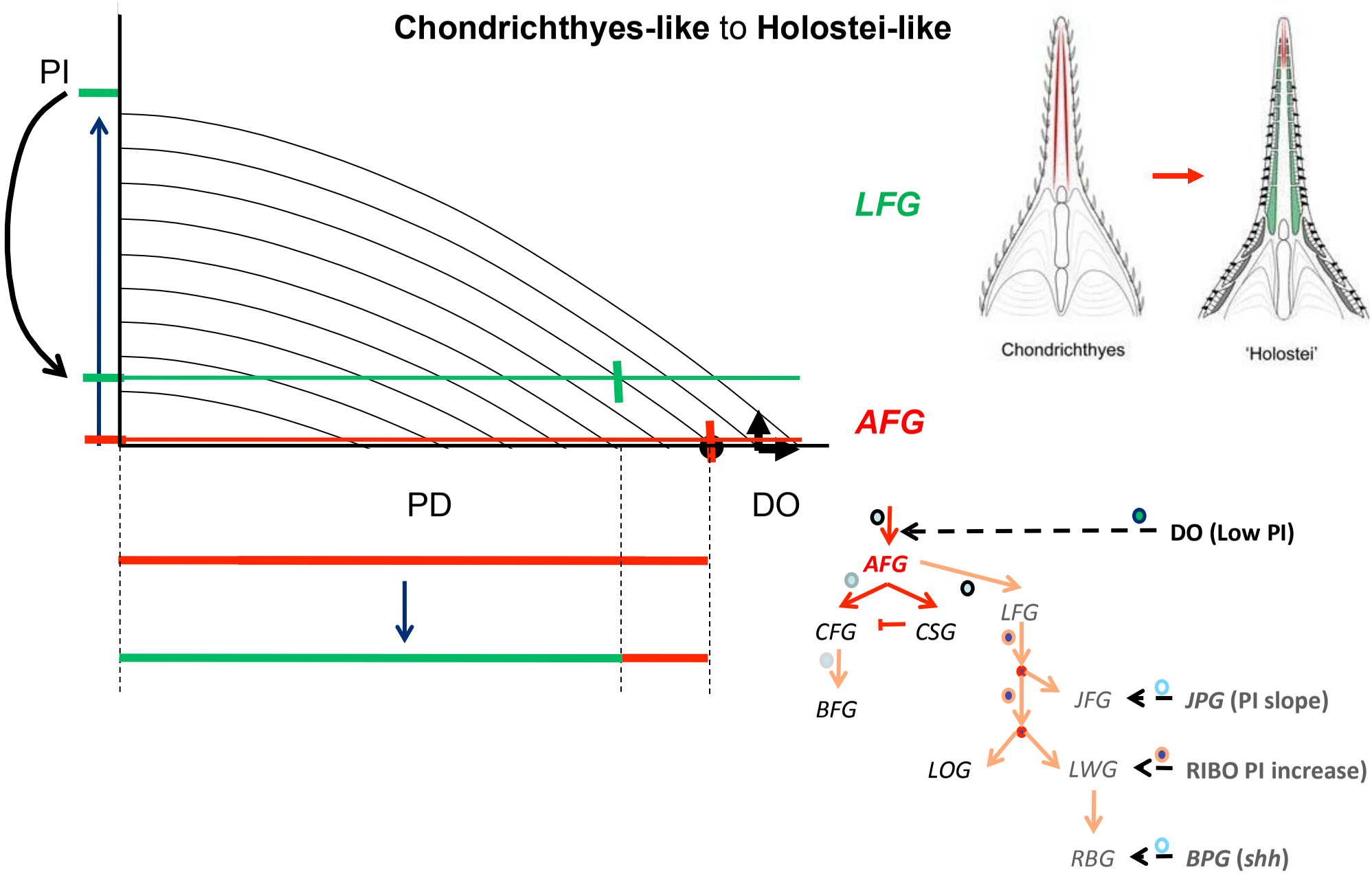
could account for this developmental series. The actinotrichia may somehow repress cartilage formation and viceversa in such a way that a third tissue is formed in the intermediate regions. In turns, lepidotrichia formin cells may initiate actinotrichia resoprtion leading to differetiation of actinotrichia in distal positions. But once lepidotrichia are formed, another genetic sequence is initiated in which distal growth, joint formation, ossification and widening sequentially appear as controlled by an initially common genetic pathway. In this case, there is no resoption of previous differentiation, or intercalary growth occurs but the addition of new elements. Lepidotrichia differentiation, lepidotrichia distal growth, joint formation, lepidotrichia ossification and lepidotrichia widening are sequentially summed to the previous actinotrichia and endoskeleton scaffold. As the gradient increases in a given distal position, de novo lepidotrichia is formed which grows distally, letting the original position in more and more proximal locations, may form joints whcih are larger proximally and shorter distally as explained in Marí-Beffa and Murciano,(2010), may ossify and finally increase in width in a sequential way. Under our model, the unique driving force is the activation of this genetic pathway by the increment of the PI gradient. Finally lepidotrichia widening could, under special conditions (Marí-Beffa and Murciano, 2010), lead to ray bifurcation depending on ray-interray interactions.

If these three genetic sub-pthways are controlled by a common body size-dependent PI gradient, a schematical developmental series may be thus proposed (Figure **) to be rigorously examined under the perspective of the geological history.

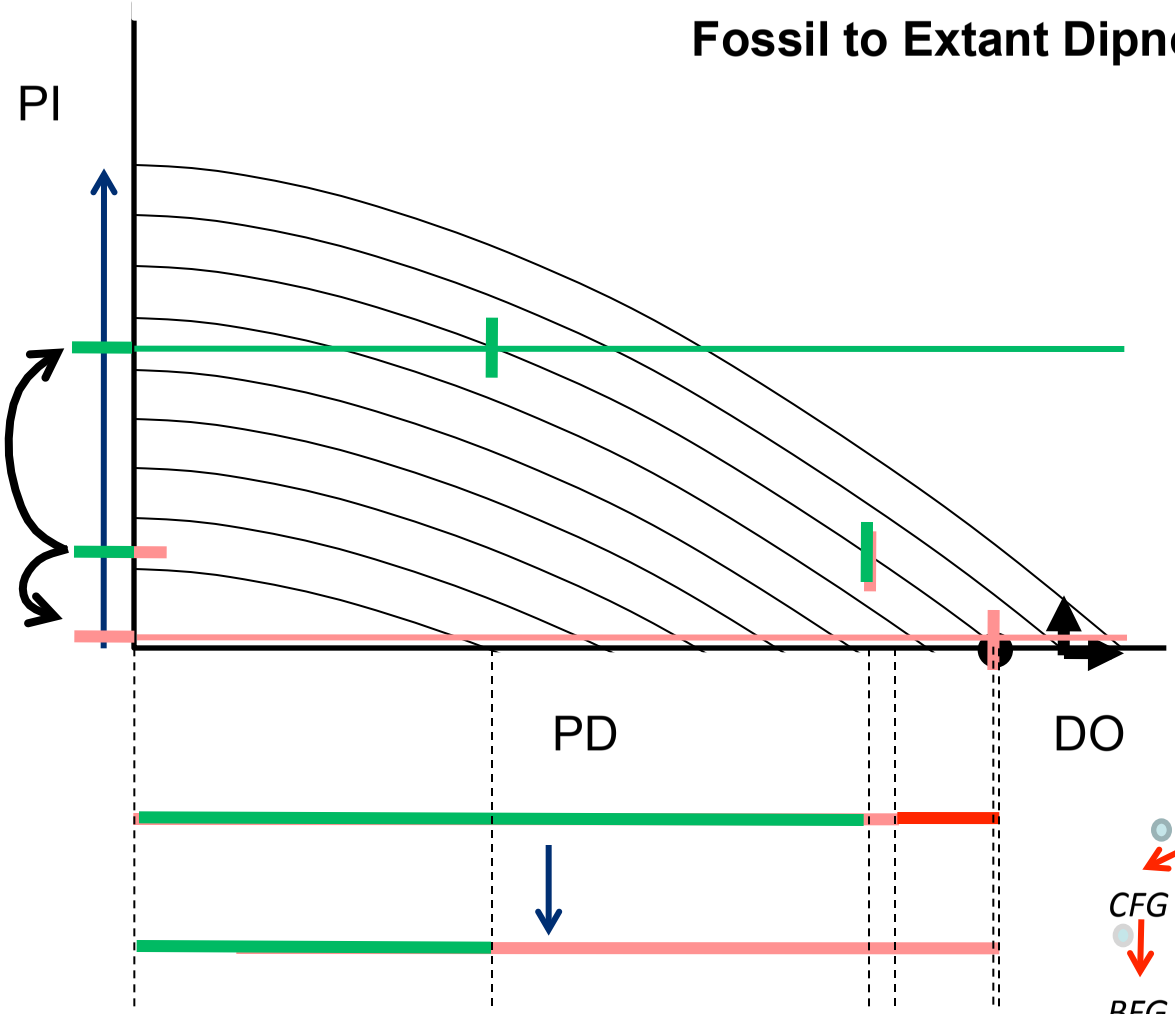
The first Actinotrichia-endoskeleton pathway could be ancient to Gnathostomata, present in chondrychthies. The second Lepidotrichia derived pathway may have evolved early in the Teleostomi lineage. In order to understand gradual distalization we may consider that the regulatory activity of the PI gradient along the differentiation pathways may vary gradually in quantity. If a lesser activation along the genetic pathway occurs all pattern elelemnts may positionally vary. More PI gradient activity would be required for any character to be differentiated and all of them would be modified to more distal positions. Hoeever, in some instances, some characters distalize whereas some others do not. This could be understood as variations in the regulation of the pathway by the other joint positioning, lepidotrichia ossification, or ray-interray boundary control. If a scale differentiation or bone size control is indepndently perturbed independent variations might occur in the different lineages.

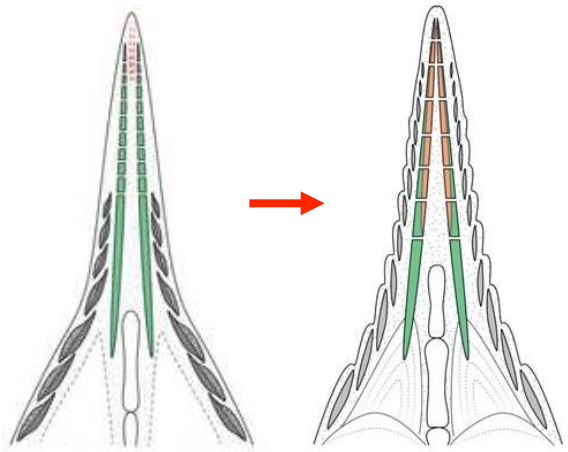
Many genes have been studied to account for part of these genetic pathways so that a complete experimental design to resolve the intricate genetic pathway may be a primary experimental goal.

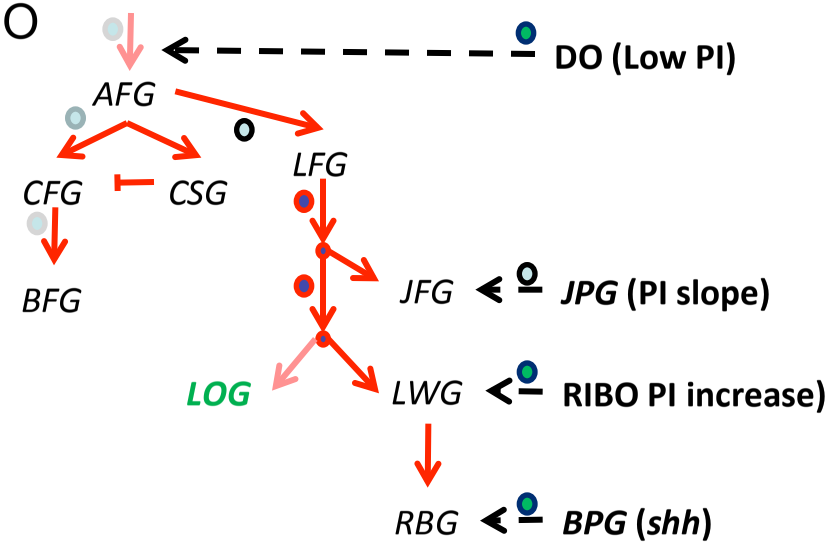

Distal Organizer (Low PI)
Actinotrichia forming genes
Cartilage forming genes
Cartilage size genes
Bone forming genes
Lepidotrichia forming genes
Joint forming genes
Joint patterning Genes (PI slope)
Lepidotrichia ossification genes
Lepidotrichia widening genes
Ray-Interray boundary Organizer (any PI increase)
Ray branching genes
Branching patterning Genes (shh)
Activated by PI ( Substitution, addition, fluctuation)
Checkpoint Control of PI activity


Chondrichthyes-like to Holostei-like
PI
LFG
AFG
PD
DO
Chondrichthyes
'Holostei'
DO (Low PI)
AFG
CFG
CSG
LFG
BFG
JFG
JPG (PI slope)
LOG
LWG
RIBO PI increase)
RBG
BPG (shh)

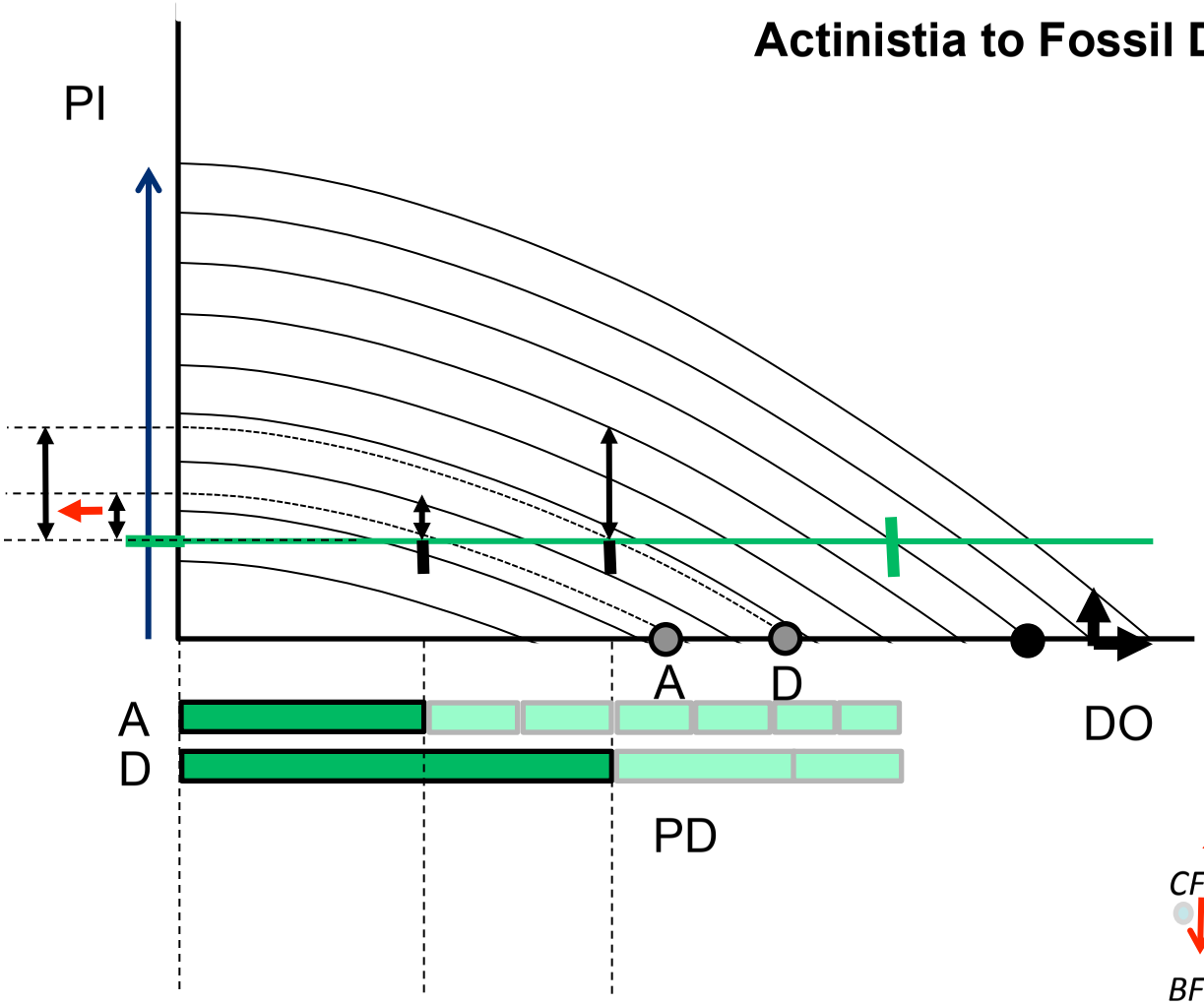
# Fossil to Extant Dipnoi

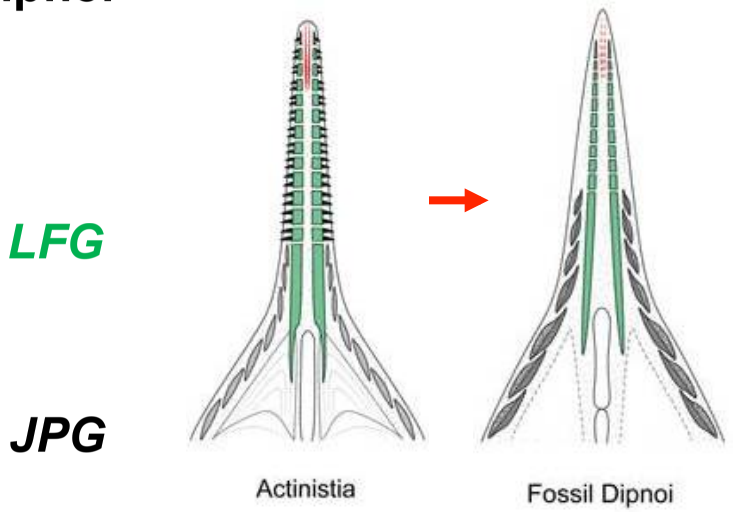


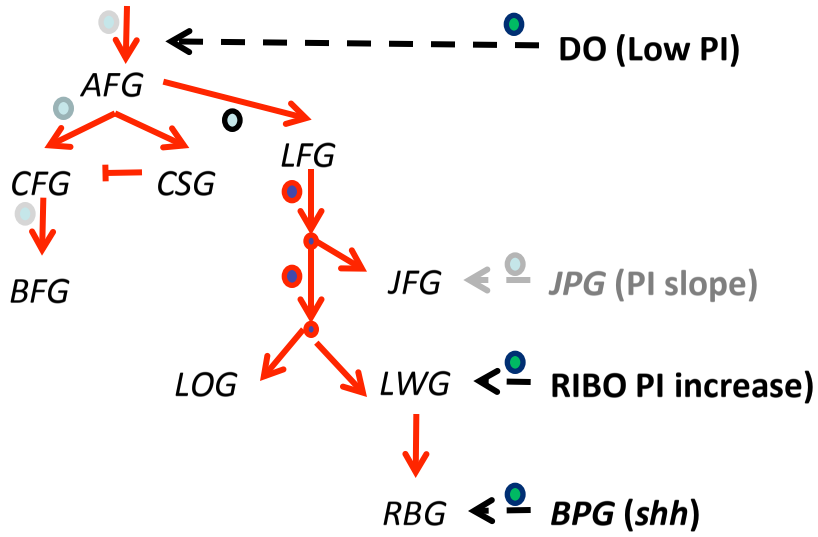



# Actinistia to Fossil Dipnoi



## **APPENDIX. IX.** List of figures

**CHAPTER I**

### II. The Devonian



### III. The Sarcopterygians



### IV. The 'Fish-Tetrapod Transition'



### V. The Dermoskeleton

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**II. Methods**



**CHAPTER III**

**CHAPTER V**

**II. On Cosmine**



**III. Transition from Rhombic to Rounded Scale Morphotype**



**IV. Squamation Evolution in Tetrapods**



**V. On the Homology Between Scales and Lepidotrichia**



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## Abstract

The origin of tetrapods and their transition to land are one of the most fundamental episodes in the evolutionary history of vertebrates. The evolution of tetrapods is characterized by the appearance of fingers, progressive reduction and disappearance of the dermal fin rays (lepidotrichia), and loss of body scales. Nevertheless, some early forms like *Acanthostega, Ichthyostega* and *Tulerpeton* from the Late Devonian retain fin rays in their caudal fin and small scales in the ventral region. The evolution of the dermal skeleton is a fundamental aspect of the 'fish-tetrapod transition', but remains largely unexplored. This pluridisciplanary thesis includes new data on Devonian sarcopterygians and from the developmental biology of extant actinopterygians. The use of new imaging techniques (CT and synchrotron) enabled to access information on the structural and developmental evolution of the scales and the lepidotrichia in sarcopterygians.
The study of the squamation in the porolepiform *Heimenia* has shown that the growth of the overlapped areas of the scales played a major role in the transition from a rhombic to rounded scale morphotype in sarcopterygians and that derived character states related to squamation in osteichthyans generally begin in the anterior region of the body. New data on the scales of the Devonian tetrapod *Tulerpeton* show that tetrapod scales are histologically and morphologically different from that of related tetrapodomorph fishes, suggesting that changes between the 'fish-like' sarcopterygian scale condition and the 'tetrapod-like' scale condition arose during the Devonian in an aquatic environment and were essentially unmodified in tetrapods during their establishment on land in the Carboniferous.
The diversity of fin ray morphologies in sarcopterygians has been reviewed and presented in detail and the consideration that developmental modifications might be responsible for this structural diversity has led to the establishment of a new framework of study, in which morphological and developmental variations of the fins and fin rays in osteichthyans should be interpreted and described under three developmental axes (proximo-distal, antero posterior, and contralateral). New evidences corroborates that lepidotrichia are not modified scales, although both structures share similar developmental features that suggest a deep homology of their morphogenetic system. The loss of the lepidotrichia in the paired appendages of tetrapods can be viewed as an inherent developmental process of distalization and loss of structures in the fins. The retention of a 'fish-like' tail supported by fin rays in Devonian tetrapods (e.g., *Acanthostega* and *Ichthyostega*) suggests that the caudal region of fishes might be more resilient to morphological changes.



**Key words**: Sarcopterygians, Devonian, tetrapods, evo-devo, scales, lepidotrichia, paleohistology, synchrotron



## Résumé

La origine des tétrapodes et la sortie des eaux sont des événements majeurs dans l'histoire évolutive des vertébrés. L'évolution des tétrapodes se caractérise par l'apparition des doigts, la réduction des rayons dermiques (lépidotriches) et la perte des écailles. Cependant, des formes basales comme *Acanthostega, Ichthyostega* et *Tulerpeton* conservent encore des lépidotriches sur la nageoire caudale et des écailles sur la partie ventrale. L'évolution du squelette dermique constitue un aspect fondamental de la 'transition poissons-tétrapodes', mais son étude demeure encore largement inexplorée. Dans une approche pluridisciplinaire, cette thèse inclut des nouvelles données sur des fossiles de sarcoptérygiens dévoniens et des données issues de la biologie du développement de poissons actinoptérygiens actuels. L'application de nouvelles techniques d'imagerie (CT-scan et synchrotron) ont permis d'accéder à un grand nombre d'informations sur l'évolution structurale et développementale des écailles et des lépidotriches des sarcoptérygiens.
L'étude de la squamation du porolépiforme *Heimenia* a montré que la croissance de la région antérieure recouverte des écailles a joué un rôle majeur dans la transition morphologique d'un morphotype rhombique vers un morphotype arrondi chez les sarcoptérygiens, et que les caractères dérives concernant la squamation se présentent souvent dans la région antérieure du corps des ostéichtyens. De nouvelles données sur les écailles du tétrapode Dévonien *Tulerpeton* montrent que les écailles des tétrapodes sont histologiquement et morphologiquement différentes de celles de leurs proches parents, les poissons tétrapodomorphes, indiquant que les changements produits entre les écailles 'de type poisson' et les écailles 'de type tétrapode' sont apparues au Dévonien dans un environnement aquatique et ont été retenues sans modifications majeures chez les tétrapodes pendant la sortie des eaux au Carbonifère.
Une révision détaillée de la diversité morphologique des rayons des nageoires chez les sarcoptérygiens a été présentée et la considération de changements dévelopmentaux comme responsables de cette diversité a conduit à la mise en place d'un nouveau cadre d'étude dans lequel les variations morphologiques et développementales devront désormais être interprétées et décrites le long de trois axes du développement (antéro-postérieur, proximo-distal et contralatéral). De nouvelles évidences montrent que les lépidotriches ne sont pas des écailles modifiés, mais que néanmoins ces deux structures partagent des charactéristiques développementales similaires indiquant une homologie profonde de leurs systèmes morphogénétiques. La perte des lépidotriches chez les tétrapodes a été envisagée comme un processus de distalisation et perte de structures dans les nageoires inhérent au développement. La présence d'une queue 'de type poisson' soutenue par des rayons chez les tétrapodes dévoniens (e.g., *Acanthostega* et *Ichthyostega*) indique que la région caudale des poissons est plus résistante aux changements morphologiques.



**Mots clés**: Sarcoptérygiens, Dévonien, tétrapodes, evo-devo, écailles, lépidotriches, paléohistologie, synchrotron

## Resumen

El origen de los tetrápodos y su salida del agua son episodios fundamentales en la historia evolutiva de los vertebrados. La evolución temprana de los tetrápodos se caracteriza por la aparición de los dedos, la reducción de los radios dérmicos de las aletas (lepidotriquias), y la pérdida de las escamas. Sin embargo, formas basales como *Acanthostega, Ichthyostega* y *Tulerpeton* todavía conservan radios lepidotriquios en la aleta caudal y escamas dérmicas en la parte ventral del cuerpo. La evolución del esqueleto dérmico constituye un aspecto esencial de la 'transición peces-tetrápodos', pero su estudio ha sido muy poco explorado. Desde un punto de vista pluridisciplinar, esta tesis incluye nuevos datos anatómicos a partir de descripciones de fósiles de sarcopterigios devónicos y datos obtenidos a partir del estudio de la biología del desarrollo de peces actinopterigios actuales. El uso de nuevas técnicas de observación (CT-scan y synchrotron) ha permitido acceder a una gran cantidad de información sobre la evolución estructural y del desarrollo de las escamas y lepidotriquias de los sarcopterigios.

El estudio del porolepiforme *Heimenia* ha mostrado que el crecimiento de la región anterior de las escamas tuvo un papel muy importante en la transición morfológica entre el morfotipo rómbico y el morfotipo redondeado en los sarcopterigios, y que los caracteres derivados relativos a las escamas de los osteíctios suelen aparecer primero en la parte anterior del cuerpo. Nuevos datos sobre las escamas de tetrápodo del Devónico *Tulerpeton* muestran que las escamas de los tetrápodos son morfológicamente e histológicamente diferentes de las peces tetrapodomorfos a partir de los cuáles evolucionaron, y que dichas diferencias entre escamas 'de tipo pez' y escamas 'de tipo tetrápodo' aparecieron en el Devónico en el medio acuático y fueron conservadas y muy poco modificadas durante la transición definitiva al medio terrestre por los tetrápodos del Carbonífero.

La diversidad morfológica de los radios de las aletas de los sarcopterigios ha sido revisada y detallada. La idea de que cambios en el desarrollo son los responsable de dicha diversidad ha llevado a proponer un nuevo marco de estudio según el cual las variaciones morfológicas y del desarrollo deberían ser explicadas y descritas en función de 3 ejes del desarrollo de las aletas (antero-posterior, próximo-distal y contralateral). Nuevas observaciones muestran que las lepidotriquias no son escamas modificadas, sin embargo ambas estructuras comparten una homología profunda de sus sistemas morfogenéticos. La pérdida de las lepidotriquias en los tetrápodos puede considerarse como un proceso de distalización y pérdida de estructuras inherente al desarrollo de las aletas. La presencia de una cola 'de tipo pez' con radios lepidotriquios en los tetrápodos del Devónico (e.g., *Acanthostega* e *Ichthyostega*) indica que la región caudal de los peces es más resistente a los cambios morfólogicos durante la evolución.



**Palabras clave**: Sarcopterigios, Devónico, tetrápodos, evo-devo, escamas, lepidotriquias, paleogistologia, synchrotron